The Trees' Influence on Soil Development.

Nutrient Cycling Strategies of Trees.
A Basis of Knowledge,
necessary for synecological
Forest Ecosystem Management.

H. J. JANSSEN

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I

With Love for Ace Vedar and Rata,
our children, and the progeny of life.

Foreword:

A concept of co-operation,
to sustain the capacity for yield,
in order to satisfy the requirement of future human generations,
without compromising the needs of other life-forms.

ABSTRACT:

The influence of various tree species and - genera on an initially homogeneous soil substrate has been analysed and compared.

The homogeneity of the site is due to a common loessial soil substrate, a narrow topographical and climatical range, the prehistoric lowland forest cover and an equivalent subsequent history with clearance of the indigenous vegetation, followed by reafforestation around the turn of the century.

The trees were located at random and soil samples were taken, half way between the trunk and the drip lines at four locations and at three depths within the soil A - horizon.

The four sample locations around each tree were pooled and the three depths at {0-1 cm; 7-8 cm; 14-15 cm} were subsequently analysed for:

pH; cation exchange capacity; contents of the base cations

$(Ca^{2+}; Mg^{2+}; K^+; Na^+)$; phosphorus;

and soil organic matter,

specifically carbon; nitrogen and the humic matter fractions, including an elemental analysis (C, N and H) of the humic fractions.

For each depth level, these soil parameters (except the elemental contents of the humic fractions) were subjected to statistical analyses {Principal Component Analysis, (P.C.A.); Cluster Analysis, (C.A.)}, which grouped individual trees into two related groups and one significantly different group according to their influence on the soil.

Analyses of Variance established hypotheses with regard to group specific nutrient cycling strategies.

A correlation analysis of all soil parameters and a regression analysis of two soil parameters aided with the interpretation of the ordination results.

An elemental analysis of the humic fractions showed differences in structure and the elemental allocation , dependent on the phanerophyte input and soil depth.

The first two P.C.A. derived groups,
New Zealand Indigenous Trees (*Dacrydium cupressinum, Prumnopitys ferruginea, P. taxifolia, Nothofagus fusca, N. solandri, N. truncata, Plagianthus regius, Sophora microphylla, Kunzea ericoides*) and **exotic Deciduous Trees** (*Acer pseudoplatanus, Aesculus hippocastanum, Fagus sylvatica, Fraxinus excelsior, Quercus canariensis, Q. robur, Q. rubra, Tilia europaea, Ulmus procera, Ulmus x hollandica*) have in common a strategy that increases the nutrient storage capacity and which favours the cycling of nutrients in the soil medium.

Individual vigours in the cycling of nutrients and the creation of nutrient storage capacity towards one or the other soil humus type are indicated by the ordinations, specifically the C.A.

The histograms, the correlation and regression analyses of soil parameters demonstrate the presence of specific strategic and amplitudinal distinctions in creating storage capacity and in the cycling of nutrients, that, based on site homogeneiety are independent from the quality of the mineral substrate.

Trees from both groups show convergences and specific inherent contributions towards the genesis of soil nutrient storage capacity and the cycling of nutrients.

A third group is significantly different from the indigenous and deciduous groups and includes the following trees *Pinus radiata, Pseudotsuga menziesii, Larix decidua, Eucalyptus regnans.* A tight clustering in the ordinations, comparison with the mineral substrate reserves, the analyses of variance, soil parameter correlation and - regression analyses demonstrate a common strategy based on the extraction of nutrients from the soil.

Nutrient extraction strategies ensure survival in the harsh environments of their natural habitats.

These trees have in common an adaptation to recurring events of disturbance, often caused by fire, which is fuelled by a litter load that resists decomposition.

An ecological term describes these as **Pyrophanerophytes** {Fire Trees}.

Fire trees tend to form stands of little species diversity.

The common transplantation of fire trees to forest-soil systems, that were based on nutrient cycling and consequently attained large soil nutrient stores will have the following consequences:

1. The growth of fire trees is faster than in their natural habitat.
2. A de-coupling of the nutrient cycling process ensues.

3. Pyrophanerophyte litter leachates and root exudates lead to the effective decomposition of clay minerals and deminishes mineral nutrient reserves.
4. Soil organic nutrient stores may be decomposed and serve as a source of N (de-coupling of the nitrogen cycle).
5. The storage decrease due to the loss of soil organic matter diminishes the cation exchange capacity and the nutrient adsorption capacity.
6. Artificial fertilisation will rapidly lose effectiveness.
7. The resulting potential for soil acidification is considerable and the soil buffer capacity may rapidly degrade to the aluminium / iron buffer range.
8. The loss of soil organic matter and biological activity may lead to a compacted physical soil structure.

These effects result in a rapid degeneration to a podzol and are the main reasons why evolution did not lead to the dominance of firetree species, since fire trees would naturally eliminate themselves by rapidly changing the soil state.

Fire trees are alien to a New Zealand oceanic-temperate forest ecosystem.

Widespread commercial forestry, based on pyrophanerophytes (fire trees) is unsustainable.

The strategies of trees from the indigenous or exotic deciduous forests show a common ecosystem strategy, based on the creation and maintenance of nutrient storage capacity and the cycling of nutrients in the soil medium, which provides the basis for a long-term potential for yield and the sustainable management of productive forests.

PREFACE

The fate of humankind is linked with its ability to embody the linear thinking of the rational mind into the cyclic ecological processes of life.

"The understanding of ecosystems is hindered by the very nature of the rational mind. Ecological awareness, arises from an intuition of non-linear systems" (Fritjov Capra, 1982).

Life organises itself at the interface of the solid, the liquid, the gaseous matter and the electromagnetic energy.

Life processes can best be visualised as a spiral, i.e. a cycle in four dimensions.

The spiral is evident in the movement of liquid and gaseous matter along gradients of pressure and time. It is manifested in the D.N.A., the structural growth of a tree, the frond of a fern, the shells of molluscs, the recurring events in the evolution of life and cultures, the movement of the earth around the sun and around the centre of the galaxy (Schwenk, 1976).

Life attempts to maintain complex structures and conserve energy, and thus slow the process towards entropy.

The beginning of a succession is strongly affected by climatic and geological factors. A pedogenesis is initiated with the cycling of matter, derived from the production of autotroph organisms and the decomposition and mineralisation by heterotrophs. The autotroph - heterotroph cycle is the driving evolutionary force of life.

The soil is as such a manifestation of the evolutionary success of a particular association.

The more complex the biological structures are, the more effective are the positive feedback "mechanisms", first with regard to the pedogenesis and the microclimate, then to the macroclimate, by way of altering the albedo and the evapotranspiration, which induces further positive feedback by extending favourable conditions for life in neighbouring regions (Walter, 1985; Reichholf, 1990).

Life on earth is based on the autotrophs and their ability to create structure by combining matter and energy.

The most complex, cooperative autotrophic structures on earth are trees.

As such, trees are the manifestation of life's establishment on the earth's landmass.

The mass of forest ecosystem components provides the inertia against environmental perturbations.

Temperate forest ecosystems may include gymnosperms, broad-leaved evergreen angiosperms or deciduous angiosperms and are spread through disjunct regions of moderate climate in the mid-latitudes of the northern and southern hemisphere and exist as altitudinal islands throughout the tropical and subtropical regions of the ecosphere (Walter, 1985).

1) The primary global determinants of temperate forest occurrence are climatic factors.

General prerequisites for temperate forest growth are a positive precipitation to evaporation ratio and moderate annual and daily temperature amplitudes (Holdridge Life Zone Classification scheme, in; Groombridge, 1992).

The seasonality of the climate is a factor, generally recognised as having been the cause of evolutionary adaptations towards soil nutrient storage capacity (Roehrig; Ulrich, 1991).

2) The secondary determinant comprises the mineral availability of the geological substrate, both of which influence the initial species composition.

3) The temporal and spatial species composition determines the pedogenesis, which in turn influences the species composition, determining further pedogenesis (Swift, 1979; Jenny, 1980; Stevenson, 1986; Ulrich, 1987).

On a spatial and temporal scale temperate forest ecosystems are highly dynamic entities (Delcourt, 1987). Trees grow in various associations in climatically diverse and spatially distinct environments.

Extremes of climatic parameters can be thousands of kilometres apart and organisms within the temperate biome replace each other gradually.

In New Zealand, a highly diverse physical environment and a maritime cool to warm temperate climate combine to provide an abundance of niches. This is reflected in the diverse indigenous flora, which mainly co-evolved with birds and a saprophytic meso- and microfauna.

This thesis investigates the nutrient cycling tendencies of some of the trees of the temperate forests biome in the New Zealand.

Research on the influence of vegetation on soil in the Dunedin area was first discussed by Thomson and Simpson (1935). They conducted research on the soil pH immediately under various indigenous trees and concluded that;

> "each species definitely influences the reaction of the soil in its immediate vicinity."

Koslowska's (1934) results on plants growing in nutrient solutions with different degrees of pH led her to conclude that plants possess the power of changing the reaction of the medium, and that:

> "species occurring in the field within the limits of narrow pH ranges characteristic of particular plant associations exhibit very clearly both the power of alkalising acidic and acidifying alkaline liquids."

Thomson and Simpson further suggested that it was

> "as important to consider the influence of the plant on the habitat as to examine the influence of the habitat on the plant-covering....Investigations on the power of different species within an association to control or at least to modify the pH value of the soil in their immediate neighbourhood appear to provide a fruitful method of attack....We consider that the data obtained show that this modifying power of the plant is a very real one."

Raunkiaer (1922) is quoted by Thomson and Simpson, as remarking that;

"if it can be proved that a species or a formation....affects the pH values of the soil in a definite direction, we shall then have demonstrated one of the factors which may be co-determinant when a given formation in the course of time alters its environment and by that means brings about its own downfall; it alters in fact the environment in favour of another combination of species."

Thomson and Simpson conclude that their study is in agreement with Raunkiaer's research and that an association may in time, so modify its own soil reaction that the seedlings of its own members cannot become established within that association.

Jacks (1934) suggested that;

"A combination of soil and vegetation might make a better unit for natural study than either separately, but owing to the different ways in which pedology and ecology have evolved, each since has demanded a distinct training for its more specialised branches, and they are not as closely interwoven as might now be desired."

Thomson and Simpson hoped that their preliminary report might be an incentive to other workers to join in gathering data on a problem hitherto (1934) practically untouched by ecologists in New Zealand.

These remarks are astounding.

Sixty years have passed and the comments are as valid today as they were then. As Jacks stated 1934, the topic is placed unfortunately on the boundary of the two scientific disciplines of pedology and ecology and hence has been ignored. Few pedologists are sufficiently versed in the field of plant ecology and vice versa.

As sensible land management options are required today more than ever, I hope that the results of my research will initiate action to elucidate a subject that we can not afford to ignore any longer.

Biological feedback mechanisms that involve present and historical human influences on forest ecosystems are so far proving to be dangerously negative. The imminent total collapse of entire forested biomes is a startling possibility.
In future, forests can not be managed by humans who limit forest management to rotation periods that fit a fraction of a human life time.
Forests are made up of living primary producers, with life strategies (nutrient cycling) and life cycles that extend over several human generations.
Forest management practices have to adapt to temperate forest cycles in order to fulfil requirements of sustainability.

"Research needs to be directed to the ecosystem as a whole.

Only when global ecological principles are grasped will it be possible to take the correct steps to avert the dangers which threaten our environment" (Walter, 1985).

I trust that the research conducted in this thesis will provide a clear vision for future priorities in land management.

I

Table of Contents

Appendix: A (Text)

Appendix: B (Tables and Figures)

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pages 80, 86, 149, 173 - 175, 182 - 184, 191.
No information is missing, however.

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List of Figures

List of Abbreviations

μg	micro grams
a. o.	amongst others
Al	aluminium
ANOVA	analysis of variance
C	carbon
C. A.	cluster analysis
C.E.C.	cation exchange capacity
Ca	calcium
DJ	Jaccard dissimilarity index
F.A.	fulvic acid
Fe	ferrum; iron
H.A.	humic acid
H.ex.	humic extracts
H_2O^D	^{d}Distilled water
I.H.S.S.	International humic substances society
K	kalium; potassium
L	litter layer
M	molar
me %	milli equivalents %
Mg	magnesium
ml	millilitres
Myrtax	Myrtaceae; Taxodiaceae
N	nitrogen
N	normal
Na	natrium; sodium
nm	nanometer
O.D.M.	soil moisture content; oven dry at 105 ^{o} C
O.M.	organic matter
O_f	fermented organic layer
O_h	humfied organic layer
P	phosphorus
p	probablity value
P.C.A.	principal component analysis
P.N.A.P.	protected natural areas program
pH	$\log_{10} 1 / H^+$
S.O.M.	soil organic matter
SJ	Jaccard similarty coefficient
Soil A-horizon	surface organo-mineral soil horizon
Soil B-horizon	subsoil (clay)-mineral horizon
T.E.B.	total exchangeable bases

1   Introduction

In text books, plants are listed as the soil-forming factors, and the soil or soil properties are listed under the factors determining plant growth. If, however, both influence each other they cannot be considered as mutually independent factors. An adequate approach is thus to view plants and soils as components of a larger entirety, the ecosystem. Ecosystem analysis has two goals: explanation and prognosis. Prognosis is a central goal in a world where all ecosystems are influenced by man. The precision of prognosis increases with increasing understanding of the system.

The goal to be reached first is therefore the explanation of the temporal behaviour of the system under varying environmental stress and under manipulation (Ulrich, 1987).

The influence of the geologically determined mineral composition and climatically co-determined weathering processes on the succession of a plant community may persist for tens of thousands to millions of years (Jenny, 1980; Molloy, 1988). This reflects a quasi steady state, which is relatively uneffected by human manipulation.

The time scale of the influence of plants on the genesis of soil is measured in anything from yearly cycles to hundreds and thousands of years.

The active involvement of plants in the development of soils has either been ignored or has been analysed from a crop perspective, rather than an ecosystem perspective and has resulted in an accumulation of information, which is much too detailed for sustainable land management decisions.

This thesis endeavours to explain the influences of trees on the genesis of the pedon. It may yield information that permits conclusions with regard to both the temporal behaviour of forest systems and some of its individual component species. Knowledge of this kind will be essential for future management objectives.

The presupposition of a correlation between plant litter quality, decomposability, and the potential for soil fertility, (Daniel, Adams, 1984) presented various options for data collection, all of which required a homogeneous soil substrate, in order to provide comparable data.

One option involved the measurement of the chemical composition of the plant litter. However, the collection of representative and comparable plant litter samples, was

impossible to achieve within the anticipated time frame of this research, since there are definite seasonal and annual fluctuations of litter contributions, quantitatively as well as qualitatively.

Another option would involve assessments of soil fauna and flora, which would be indicative of the quality of tree litter and of the potential of symbiotic associations between primary producers and the soil fauna. However, little research has so far focussed on an assessment of soil biota differences in New Zealand, since the methods of data collection seem cumbersome at present and questions concerning the homo- or heterogeneity of the various biomes with regard to the soil biota limited the interpretability of potential results.

A method which emerged, comprised a "snap-shot sample" of the soil A-horizon immediately underneath trees, half way between the trunk and the dripline and at three depths, followed by an elemental analysis of soil nutrient content and a focus on the most stable organic compounds therein.

The research hypothesis was to examine whether various trees, as the prominent primary producers, exert a measurable influence on the soil A-horizon chemistry of a homogeneous mineral soil substrate.

Significant findings will be discussed in the context of synecological - and autecological strategies.

Chapter 2 describes the environmental setting, the survey areas, the sample sites and trees.

Chapter 3 outlines the sampled floral composition in the vicinity of the trees. In chapter 4 data on organic litter layers is depicted, commented on and the methods of soil collection are described.

Chapter 5 informs on the analysis techniques for various soil parameters.

Chapter 6 describes the statistical analyses of soil parameters, including ordinations of principal components and cluster analyses, the analyses of variance and correlations of soil parameters to further elucidate the results, obtained from the ordinations and the ANOVA.

Chapter 7 informs on the results of the elemental contents of the humic fractions.

Chapter 8 discusses the findings in the wider context of contemporary research.

Chapter 9 concludes by conferring the ramifications of the results

Chapter 10 presents a recommendation with regard to sustainable land management practices.

Appendix: A provides additional information on the locality (1) and elucidates the ecological origins of the examined species (2).

Appendix: B contains tables and figures with additional relevant information.

2   Study area and study sites;

2.1   The Dunedin Ecological District.

2.1.1 Location and Topography

The Dunedin Ecological District is part of the Otago Coast Ecological Region (P.N.A.P.1987). The Otago Coast Ecological Region covers the south eastern coastal land of the South Island of New Zealand. It extends from the Shag river in the north to the coastal Clutha river lowlands in the south. The Region extends inland for 20 to 30 kilometres, parallel to the coast line with the South Pacific Ocean and more or less along the tops of the coastal ranges.   The main parameters, that define the Otago Coast Ecological Region are a common climate and a prehistoric cover of broadleaf - podocarp forest.

The Dunedin Ecological District is characterised by the following homogenous features: the loess covered, volcanic base material; the hilly, undulating to rolling topography; the local cool and moist climate with frequent fogs above 400 meters and the prehistoric broadleaf podocarp forest cover.

The Dunedin Ecological District comprises some 460 km^2 of well dissected Miocene volcanic terrain with whale-backed hills and eroded calderas, up to an elevation of 739 meters.

The district extends from latitude 45° 43' S to 45° 56' S and from longitude 170° 21' E to 170° 45' E. The area as a whole protrudes about 20 kilometres from the coastline of the Otago Coast Ecological Region. The inland boundary of the district commences at the Kaikorai lagoon in the south and follows the Abbotts creek north to the base of the western slopes of Abbotts Hill and Flagstaff Hill (361 m and 668 m respectively). From the Silverstream valley at the base of the western slopes of Flagstaff Hill the inland boundary swings to the north - west, following the western margin of the Swampy Summit and Hightop Hill (739 m and 531 m respectively) and meeting the coast immediately north of Blueskin Bay.

The hills of Dunedin city, to the east of the Kaikorai valley reach a height of 100 to 200 meters. The hills of the Otago Peninsula range to 400 meters and the line of extinct volcanoes to the north-east of the Otago Harbour reaches heights of up to 676 meters (Mount Cargill).

The major topographic features of the Dunedin district are the result of very late or post - Tertiary crustal movements (Benson, 1941). The crustal movements were

comparatively small prior and during most of the period of eruptive activity (see 2.2), but reached their climax during and after the cessation of the eruptive phase. Some Pleistocene valleys of the terrain and the syncline of the Otago Harbour have been submerged during the Holocene marine transgression. The sheltered Otago Harbour and several smaller inlets and bays, with dune backed beaches at the exposed coast bear witness to the coastal dynamics of the district during the Holocene.

2.1.2 Geology and Geomorphology

Most recent soils in the Dunedin Ecological District have formed on, or in conjuncton with layers of loess. The loess cover varies in thicknesses, dependent on topography and aspect. The loess layers were deposited during the glacial stadia of the Pleistocene. Loess is an aeolian deposit, other than sand dunes, of fine sandy loam structure or finer (Raeside, 1964).

Contrary to most overseas loess deposits, New Zealand loess deposits are compact, of low permeability, non-homogeneous and non-calcareous. There appear to have been six phases of loess deposition, each followed by a period when no loess, or only an insignificant amount, was deposited. With few exceptions, the South Island loess is uniformly a silt loam and the soils have been classified as yellow-grey earths with a fragipan, showing distinct stratification in the drier areas of Canterbury, and grading to yellow-brown earths, showing less stratification with increasing rainfall in eastern Otago and Southland (Raeside 1964; Molloy 1988).

The loess of the Dunedin Ecological District is mainly derived from the metamorphic rocks of Otago. Quarz and plagioclase feldspar in roughly equal proportions make up from 70 % to 80 % of the primary minerals. Mica and chlorite may amount to as much as 7 % , and minor accessory minerals consist of epidote, tourmaline, zircon, amphiboles, sphene, iron ores, plant opal and sponge spicules (Raeside 1964). Loess deposits at the seaward side (Harrington Point, Otago Peninsula) indicate that some loess derived from sources located on the continental shelf during sea - level recessions of the Pleistocene. Stratified lower slope deposits of fragments of local rocks and loess, derived from the metamorphic schists of Otago, filled the drainage system and settled on the flanks of the Dunedin hills. This points to an active solifluxion (caused by freeze-thaw action) during the glacial cycles of the Pleistocene. The lowermost solifluxion layer consists chiefly of weathering products of local igneous rock. The proportion of loess increases towards the top of the solifluxion deposit, with the top of the layer being largely loess. This may be indicative of loess deposition continuing into the early parts of the interglacials (Raeside, 1964). Periods of solifluxion and loess deposition clearly alternate with periods when the surface deposits remained stable and soil processes took place without interruption. The weathering and soil-forming sequences consist of two intervals of major rank and three intervals of minor rank (Raeside, 1964), corresponding to phases of climatic warming during the Pleistocene and the Holocene. For additional information consult appendix, 1.1.

2.1.3 Climate

At 46° southern latitude the Dunedin Ecological District is situated within the southern temperate climate zone.

This zone is characterized by seasonal climate changes and dynamic weather patterns. The succession of westward moving cyclones and their associated warm air - and cold air fronts brings about the typical dynamic weather patterns. Warm air, which descended from sub-tropical anticyclones and cold polar airmasses, are subject to the coriolis force and combine in westward moving cyclones. The coriolis force is the cause of a circum-global band of winds, arriving from a westerly direction in the mid latitudes of both hemispheres.

The orography has a very dominant effect on the variation of the climate and wind flow within the country (McKenzie et al., 1976). The moist and coastal climate of the Dunedin Ecological District has been classified as having warm summers, cool winters and an evenly distributed rainfall. Frequent fogs in the uplands are due to the local topography and other factors, such as the proximity to a cold ocean current, sweeping north along the east coast of the South Island. A region of opposing semi arid and highly continental climate, lies only one hundred kilometres north-west of Dunedin, in the Lee of the Southern Alps. These skew winds in the Dunedin district to a slight predominance of winds of all speeds from either a west-south-westerly or from an east-north-easterly direction (McKenzie et al., 1976).

The mean yearly rainfall of 938 mm, ranged between 555 to 1385 mm, in the period of 1852 to 1980 (Climate Info., VAX, Univ. of Otago, 1994). Relative humidity averages at 72% annually, with monthly variations of +/- 5% in the period between 1928 to 1942. Precipitation is slightly greater in summer than in winter, the difference increasing with altitude. Snowfall is significant only above three hundred meters. Snow fell on average at 7 days at the Botanic gardens and an average of 5 days with hail was recorded annually during the period from 1863 to 1942 (Climate Info., VAX, Univ. of Otago, 1994).

The estimated range in precipitation varies from 760 mm in 160 raindays to 140 mm in 210 raindays (N.Z. Met. Serv., 1963). Mean annual temperatures at low altitude are 11° C near the coast. Annual and diurnal ranges are greater inland, where the warmest month (January) has a mean temperature of 15.5° C, compared with 4.5° C for the coldest month (July). The average daily range has been recorded as 8.2° C at the Botanic Gardens. Temperature generally decreases with altitude, but on frosty nights inversions develop, with the point of reversal below 170 m (Wardle 1953). The

records show an average of 37 days annually of ground frosts at the Botanic Gardens in the period from 1864 to 1942 and 6 days for air frost (Climate Info., VAX, Univ. of Otago, 1994). The average annual duration of bright sunshine has been reported to be 1,700 hours and the average incoming radiation is around 300 cal cm^{-2} day^{-1} (McKenzie et al. 1976).

2.1.4 Flora and Fauna

The pre-European indigenous vegetation of the Dunedin Ecological District consisted of mainly broadleaf-podocarp forest, patches of *Nothofagus menziesii* forest and small areas of shrub and grassland on coastal dunes and notably at the base of the Otago Peninsula (Tuckett, 1844).

A landscape of such topographical diversity had the potential to accommodate a multitude of ecological niches. Riparian, coastal or altitudinal ecotones were important features in this aspect.

Several tiers can be distinguished in the structure of the lowland broadleaf-podocarp forest. A ground stratum consisting of bryophytes, ferns and seedling trees. A shrub stratum, embodying a high diversity of dicotylous and divaricating shrubs and tree ferns. The main canopy of the forest consists of a variety of dicotylous species such as *Weinmannia racemosa, Griselinia littoralis, Metrosideros umbellata, Plagianthus regius*. Longlived members of the podocarpaceae (*Dacrydium cupressinum, Prumnopitys ferruginea, Prumnopitys taxifolia, Podocarpus hallii*) form an emerging strata, above the canopy of largely broadleaved species. Synusiae of epiphytes and lianas are also well established.

The 30 metres tall lowland broadleaf-podocarp forest merges at 350 to 400 metres into a 20 metres tall montane forest and this continues either to a false tree line at circa 550 metres on Flagstaff and Swampy summit or to the summit of Mt. Cargill (676 m). Only *Podocarpus hallii* among the lowland podocarps persists into the montane zone, which is dominated by *Libocedrus bidwillii*. Treeferns are absent here, but ground ferns and bryophytes are prolific throughout. The distribution of the montane forest coincides with the normal pattern of sea fogs, which can occur on up to 25 % of the days in summer. An island of *Nothofagus menziesii* forest has established in an altitudinal ecotone at Mt. Cargill and is rather uniform in character compared to the broadleaf-podocarp forest. *Danthonia flavescens* occupies higher altitudes in the west, with *Kunzea ericoides* and *Leptospermum scoparium* communities common throughout. *Poa cita* and ferns had replaced the forest to the west of the district (Wardle 1953). These communities are the result of early fires, probably pre-European.

Since 1848 most of the forested area of the district has been felled and converted to an urban settlement area, to extensive pastoralism or plantation monoculture forestry. Many exotic species were introduced, some of which are spreading quite

successfully. *Ulex europaeus* and *Cystisus scoparius* prove to be difficult to control on extensively farmed lands and potentially facilitate the process of re-afforestation.

Some exotic gymnosperms, especially *Pinus radiata*, and some *Eucalyptus* species are commercially propagated and cover ever more land, most of which used to be indigenous lowland forest land.

A variety of introduced mammals (possums, goats, rats, deer, pigs, cats, dogs, stoats etc.) and insects (wasps, bees) put the remnant indigenous biota under extreme pressure.

Indigenous forest biota are very small and fragmented in the Dunedin Ecological District today. While the forests of this district were destroyed during the historical times of European settlement, the isolation of the forested Dunedin district, from forests in the Catlins region and Southland, as well as Canterbury in the north, was a result of fires during the times of Polynesian settlement in the South Island (Trotter, McCulloch, 1989).

For additional information please consult Appendix: A 1.2.

2.1.5 Cultural Influences

The Maori population has been estimated to have numbered around 5000 in Otago-Southland in 1810-1830. Large Maori settlements existed in Karitane, Otakou, and the Taieri mouth, the combined coastal population within this area, prior to outbreaks of epidemics, has been estimated to have been between 1500 to 2000 in 1830 (Goodall, Griffiths unpubl. report "Maori Dunedin" Hocken Library, Dunedin). Initially the sea and the avifauna provided the main source of food. After contacts with European Whalers, potatoes were cultivated and pigs were held in the forests.

Frederick Tuckett was sent by the New Zealand Company in 1844 to recommend suitable sites for urban settlement in the South Island. He decided the upper part of the Otago harbour would be superior to any other site he had examined along the east coast.

The main reason for this decision being the abundance of timber for building and the arable hinterland of the Taieri plains and the Clutha (Hocken exhibition 1994). An extract from his diary reads:

> "On either side of the Otago harbour the forest continues unbroken; good timber is abundant; the soil, notwithstanding that the surface is often rocky and stony, appears to be fertile, the rock being probably a species of basalt."(Tuckett, 27.4.1844).

The subsequent urban settlement brought about the rapid destruction of most of this unbroken indigenous forest from about 1848.

A green belt, consisting of European deciduous trees and indigenous trees, was established on the hills surrounding the city centre and the first botanic garden in New Zealand was transferred to the present 32 hectare site in 1886.

The western slopes of Flagstaff were planted mainly in exotic gymnosperms, incorporating trials of a variety of genera and today are managed, conforming to commercial interests.

A forest fire in Orokonui initiated a forest stand of *Eucalyptus regnans* in the first decades of this century.

Human activity and the aftermath of deforestation has given rise to subsequent compaction and gleying of three loessial soil series, (Tomlinson and Leslie 1977).

For additional regional information please consult the Appendix: A 1.3.

2.1.6 Soils, Genesis and Structure

The parent material of soils in the Dunedin Ecological District is loess and complexes of loess and igneous or sedimentary rocks. Variances in this foundation, as well as topographical, climatical and floral disparities form the basis of distinguishable soil characteristics.

The general survey of the South Island (New Zealand Soil Bureau 1968) identifies about 20 soil sets in the area. The most extensive being podsolised yellow-brown earths, yellow-brown earths and yellow-grey earths and their intergrades.

Soils derived only from loess are less extensive in the area, when compared to soils derived from complexes of loess and igneous or sedimentary rocks.

Of the five sampling sites for this study, four are based on yellow-grey earths, derived only from loess, while one site is based on a soil, derived from loess and phonolite. Of the former four sites three are based on the Dunedin soil series and one is based on the very similar Warepa soil series (Macintosh pers. com., 1993).

These and other local soil series have been analysed in detail by Tomlinson and Leslie (1977), who described the morphological properties of eight soil series in the Dunedin district. All eight have loess as their sole or dominant parent material. Environmental parameters of climate and altitude, vegetation and topography have been discussed and their respective influence on soil development and the distribution of the soil series. The study of the eight series, which were classified according to the New Zealand (Taylor, Pohlen 1968) and the Soil Taxonomy (Soil Survey Staff 1975) classification schemes, demonstrated a dominant influence of climate and altitude on the soil development.

According to the soil taxonomy the eight soil series classify as Inceptisols at the order level. All develop in a mesic temperature regime and have an udic moisture regime, as well as ochric epipedons and cambic B - horizons. At the suborder level seven series and all that are dealt with in this thesis are Ochrepts.

The soil series, investigated by Tomlinson and Leslie (1977) cover an altitudinal range from 3 m to 600 m. The slopes range from almost flat to rolling surfaces with generally all, but predominantly southerly aspects. These factors, but foremost the altitudinal range can be correlated to the identified dominant influences on soil development in Tomlinson's and Leslie's (1977) study. Related findings point to a

positive correlations of precipitation and organic matter content, as well as precipitation and carbon - nitrogen ratio. This indicates less efficient organic decomposition with higher rainfall and lower temperatures. Base saturation and pH values tend to decrease with higher rainfall, except in the Dunedin soil, which does not fit the rainfall pattern. Amounts of phosphorus in the soil, both in plant available form and as reserves are low. The mineral contribution to the cation exchange capacity C.E.C. is similar in most soils and is of the order of 12 to 15 me. %. This indicates that differences in the cation exchange capacity across the eight soil series are related to the content of organic matter (Tomlinson, Leslie, 1977). The authors conclude that, "while the general soil distribution is related to climate, the other factors of topography, vegetation and human activities are important in determining local patterns."

2.1.6.1 Site homogeneity, as determined by the occurrence of closely related soil series.

Introduction

Pedological prerequisites are investigated. The soils from four different survey sites are homogeneous.

Dr. P. MacIntosh provided expert advice concerning the comparability of the three soil series. The assumption was shared that all soil series can be regarded as recently homogeneous and hence have the rare potential to demonstrate qualitative influences of the vegetation on the soil.

Three indigenous trees of significance were located in a fifth survey site, which is slightly heterogeneous, when compared to the others. The trees are representative of an emergent forest strata, which survived largely unmodified as an indigenous lowland forest remnant.

2.1.6.2 Yellow - Grey Earths.

The sample sites of this study, at Opoho, the Town Belt and Flagstaff are based on the Dunedin and Opoho soil series. The sample site in Orokonui is based on the Warepa soil series. The solely loess-derived mineral base is a common feature of all named soil series. A trend towards gleying has been attributed to the clearance of the indigenous forest cover and constitutes the main basis for a grading into one or the other of the three closely related soil series (Tomlinson, Leslie 1977).

One sample site, in unlogged indigenous forest at Mt. Cargill, is based on Mihiwaka- and Tokoiti silt loam. The Mihiwaka and Tokoiti silt loam is an intergrade between yellow-brown earths and brown granular loams, derived from loess or loess and phonolite. Further characteristics of the Mi- To- silt loam soil series will be discussed separately (see 2.1.6.3.).

The Dunedin soil series has been classified as a weakly gleyed, loess derived, hygrous yellow-grey earth (Taylor, Pohlen 1968; N.Z. Soil Bureau Map 107 1978). The distinction between the Dunedin soil and the Opoho soil series is that the latter is moderately gleyed. The Warepa soil series is a moderately gleyed, loess derived, subhygrous yellow-grey earth. At the subgroup level of the soil taxonomy (Soil Survey Staff 1975) the Dunedin soil has been classified as an Umbic Dystrochrept

and the Opoho and Warepa soil series as an Aquic Fragiochrept, due to a fragipan in the C - horizon (Tomlinson, Leslie 1977). Soils of the Dunedin and Warepa series are found below 330 metres and receive 750 - 1150 mm of rain annually. The average temperature ranges between $8°$ C and $11.5°$ C for the Dunedin soil series and measures above $9.5°$ C for the Warepa soil series. The environmental parameters of the Dunedin soil series are equivalent to those of the closely related and often adjacent Opoho soil series. All three series frequently grade into each other at various localities.

The dominant matrix colour of the parent material is close to yellowish brown with a 10 YR hue, the chroma and value ranging from 4/2 in the A_1 - horizon to 6/6 in the (B_2) - horizon and 6/4 in the C_1 - horizon of the Dunedin- and Opoho soil series. The A_1 - horizon and the $B_{2(g)}$ - horizon of the Warepa series have a 2.5 Y hue and a chroma and value of 4/2 and 6/2 respectively. The colour of the C_{1x} - horizon is again 10 YR and 6/6. Other features include grey and yellowish red mottles and hard Fe, Mn concretions in the B_2 - and C_1 - horizons of the soils and reticulate brownish-grey and grey veins in the Opoho and Warepa C_1 - horizons. Contrasting grey colours in the profile reflect the intensity of gleying. The (B_2) and C_1 - horizons of the Dunedin- and Opoho soil series show only slight gleying. The $B_{2(g)}$ - horizon in the Warepa soil series is grey with reddish yellow mottles, suggestive of intermittent periods of reduction and oxidation, which reflect water saturation in winter and drying out in summer. This periodic feature is shared by the B_2 - and C_1 -horizons of the Opoho- and Dunedin soil series, although becoming less prominent. The grey veining or gammation in the C_1 - horizons of Opoho and Warepa is due to localisation and concentration of gleying down cracks (Tomlinson and Leslie 1977).

The soil consistences and textures are friable to firm silt loam in the A_1 - and B_2 - horizons respectively, grading to very firm silty clay loam in the C_1 - horizons. A very firm, silty loam to silty clay loam $B_{2(g)}$ - and C_1 - horizon distinguish the Warepa soil series. The structure of the A_1 - horizons grades from moderate fine nut and crumb in the Warepa soil over moderate to fine nut of the Opoho soil to strong medium nut in the Dunedin soil series. The structure of the B_2 -horizons is moderate medium to moderate coarse blocky in the Dunedin- and Opoho soils and moderate to medium prismatic, breaking to a coarse blocky structure, in the Warepa soil. The C_1 - horizon of the Dunedin soil is weak coarse blocky structured and moderate coarse prismatic in the Opoho and Warepa soils. Fragipans are well developed in the C_1 - horizon of the Warepa- and grading less from the Opoho- to the Dunedin soil series.

Tomlinson and Leslie (1977) suggest that the soil series would not show yellow-grey earth properties, had the indigenous forest not been cleared.

"It seems probable that under forest the greater rooting depth and smaller micro-climatic fluctuations, as compared with grassland, favour the development of yellow-brown earth characteristics. The removal of forest has resulted in a reduction of rainfall interception above ground, increasing periods of water saturation of the upper soil, which consequently became gleyed."

Decreased subsoil permeability, due to reduced deep rooting, may further encourage the gleying process. Shallow A_1 - horizons particularly in the Opoho and Warepa soil series suggest that these soils are the result of post-clearing erosion (Tomlinson, Leslie 1977).

Chemical analyses on the Dunedin and Warepa soils (Tomlinson, Leslie 1977) provide baseline data on key parameters. In the Dunedin series measurements were taken from the A_1 - horizon at a depth of 7-20 cm; from the (B_2) between 20-38 cm and from the C_1 - horizon at 38-66 cm depth. Analyses for the Warepa series were conducted from the A_1 - horizon at 2.5-18 cm depth; the A_3 - horizon at 18-36 cm depth and from the $B_{2(g)}$ - horizon at 36-61 cm depth. The findings will be discussed in conjunction with the results of this thesis.

2.1.6.3 Description of the soil of the lowland forest remnant.

The Mihiwaka and Tokoiti silt loam is a yellow-brown earth, associated with a rolling topography, and derived from loess and phonolite. The phonolite has varying chemical compositions with SiO_2 contents of 51 % +/- 3%; Al_2O_3 contents of 19 %; Na_2O contents of 8%; CaO contents of 5 %; FeO contents of 4 %; K_2O contents of 3.8 %; Fe_2O_3 contents of 3.5 %; MgO contents of 2 %; TiO_2 contents of 0.7 %, +/- 0.5 % and P_2O_5 contents of 0.5 % (Coombs, pers. com., 1993).

As a result of pleistocene solifluxion, the soil profile at the Mt. Cargill sample site shows weathered phonolite fragments, throughout the B - horizon, in a matrix of loess. The horizons lack much differentiation. At the B - horizon soil sample site of the unlogged indigenous forest the "L"-litter layer measures 4 cm and the "O"-organic layer measures 1 cm. The A - horizon grades into the B - horizon at 25 cm depth and the B - horizon into the C - horizon at 80 cm depth. The top of the C - horizon is marked by a zone of oxidation and Fe accretion.

The topsoil colour is dark brown (10 YR 3/3), the subsoil colour grades to 7.7 YR 4/4.

The topsoil texture is a sandy silt loam, grading to a silty clay loam in the subsoil.

The consistency grades from friable in the topsoil to firm-friable in the subsoil.

The structure of the topsoil is strongly developed, medium granular and nutty. The subsoil has a moderately developed, fine nutty and granular and weakly developed fine blocky structure.

A similar "Cargill"- soil has been investigated by Campbell (1970). The dominant clay minerals are vermiculite, kaolinite and allophane. Amounts of vermiculite clay minerals decrease with depth (0 - 66 cm) from 25% to 10 %; kaolinite amounts increase with depth from 20 % to 25 %, as do illites from 5 % to 10 %; allophane and hydrous micas maintain about 20 % and gibbsite maintains 5 % at all depths (Campbell, 1970).

Increases with depth of the clay content and the kaolin fraction articulate the increased effects of weathering with the depth of the profile in a mountainous area with high precipitation.

The effectiveness of the soil organic matter, in containing and cycling nutrients in the soil A - horizon under such humid conditions is of special interest, since a

considerable part of New Zealands remaining forest ecosystems survive as temperate rainforests, associated with orographic precipitation.

2.2 Site identification; Sampling design; Species description.
Indigenous and Exotic Temperate Forest Types within the Dunedin Ecological District.

2.2.1 Methods.

Random methods of sampling were applied after an initial reconnaissance of the area, using detailed soil- and if possible vegetation maps (Tomlinson, Kennedy, Leslie, 1978; Allen 1982; Macintosh pers. com., Landcare, 1993; D.C.C., 1987; City Forests, Taylor pers. com., 1993; Dunedin botanic gardens, 1989; Topomap I&J44, 1987).

The survey areas were defined by locating the common soil series and a variety of forest associations. Four out of five survey areas had a planted, secondary forest cover, accommodating various indigenous and exotic tree associations, which do not represent original ecological communities, but rather form a composite of mainly indigenous sub-canopy species with either indigenous or exotic canopy species. Consequently four forest associations were identified as growing on an initially homogeneous soil substrate, in four survey areas:

indigenous forest in Opoho I44&J44 172-6E798-802N;

mainly exotic deciduous forest at the Town Belt I44&J44 148-52E778-82N;

exotic gymnosperm forest at Flagstaff I44&J44 98-103E814-19N;

exotic australian forest at Orokonui I44&J44 223-8E906-11N.

A fifth survey area is located at Mt. Cargill I44&J44 192-6E841-5N

and comprises the only comparable local site with relatively undisturbed indigenous lowland forest.

Figure 2.1　　　　**Map of the Dunedin Ecological District, (western part),**

Inclusive of survey areas

Scale 1: 100,000

2.2.1.1 Opoho; Town Belt; Orokonui; Flagstaff.

The survey areas in Opoho and the Town Belt covered 16 ha each, in form of 400 m squares, superimposed on the forested areas. Those of the Orokonui and Flagstaff survey areas covered 25 ha each, as squares of 500 m length.

A grid of coordinates was set up over these four survey areas. Pairs of random numbers were taken to locate each of 28 points.

The points were located in the field and the quadrats were set up to the north-east of the random points and measured 5 x 5 metres. They were used to obtain descriptions of floral compositions of the lower strata forest vegetation. * (chapter 3).

The nearest individual tree, with a minimum breast height diameter of 30 cm was located from each random point. An even proximity of *Nothofagus fusca* and *N. solandri* to one point led to the establishment of one quadrat and two soil sampling sites.

2.2.1.2 Mt. Cargill.

Two quadrats and three specimens of indigenous mature podocarps were randomly located at the Mt. Cargill survey site. Difficulties in assessing the location of the site on existing maps made it necessary to determine the trees by the random walk method. The starting point was located in the field at a track sign, well within the podocarp forest. A sample tree was located by taking one predetermined random number between 0 and 360, to give a compass bearing, and another random number between 10 and 100, for the number of paces. The nearest individual podocarp with a breast height diameter of > 30 cm was selected and soil samples were taken. Once again, the proximity of two trees to one point led to the sampling of soil from both, *Prumnopitys ferruginea* and *P. taxifolia* and to the identification of one of two quadrat sites

Altogether, thirty individual trees were sampled, comprising twenty one genera and twenty six species. The Figures 2.2 provide an impression of the forests, that were surveyed and show some trees that were "amenable" to having photos taken (light and position).

2.2.2 Description of Survey areas.

2.2.2.1 The Opoho and Mt. Cargill survey areas.

Six species of indigenous trees were located at sites in the Opoho survey area, three of which were introduced to the Dunedin ecological district.

These are three species of the genus *Nothofagus*, namely *N. fusca*, *N. truncata* and *N. solandri*.

Other introduced indigenous subcanopy species include *Coprosma robusta* and *Coprosma grandifolia*. All were planted sometime after 1886, the year the Botanic Garden was established at the current site.

Care was taken to exclude specimens that obviously had been subjected to gardening activities. One indigenous specimen, *Fuchsia excorticata*, was located in the Town Belt.

Specimens of three indigenous species of Podocarpaceae were randomly located at sites in the Mt. Cargill survey area. These are *Dacrydium cupressinum*, *Prumnopitys ferruginea* and *Prumnopitys taxifolia*.

The group of indigenous, canopy-forming tree species comprises the six trees from the Opoho area, namely *Nothofagus fusca*, *Nothofagus solandri*, *Nothofagus truncata*, *Plagianthus regius*, the seral *Kunzea ericoides*, *Sophora microphylla*, the three trees from the Mt. Cargill area are *Dacrydium cupressinum*, *Prumnopitys ferruginea* and *Prumnopitys taxifolia* and one tree, *Fuchsia excorticata* from the Town Belt survey area (Poole, Adams, 1979).

Figure 2.2 a.

2) *Prumnopitys taxifolia*

1) *Dacrydium cupressinum*

Figure 2.2 b.

2) *Nothofagus solandri x solandri*
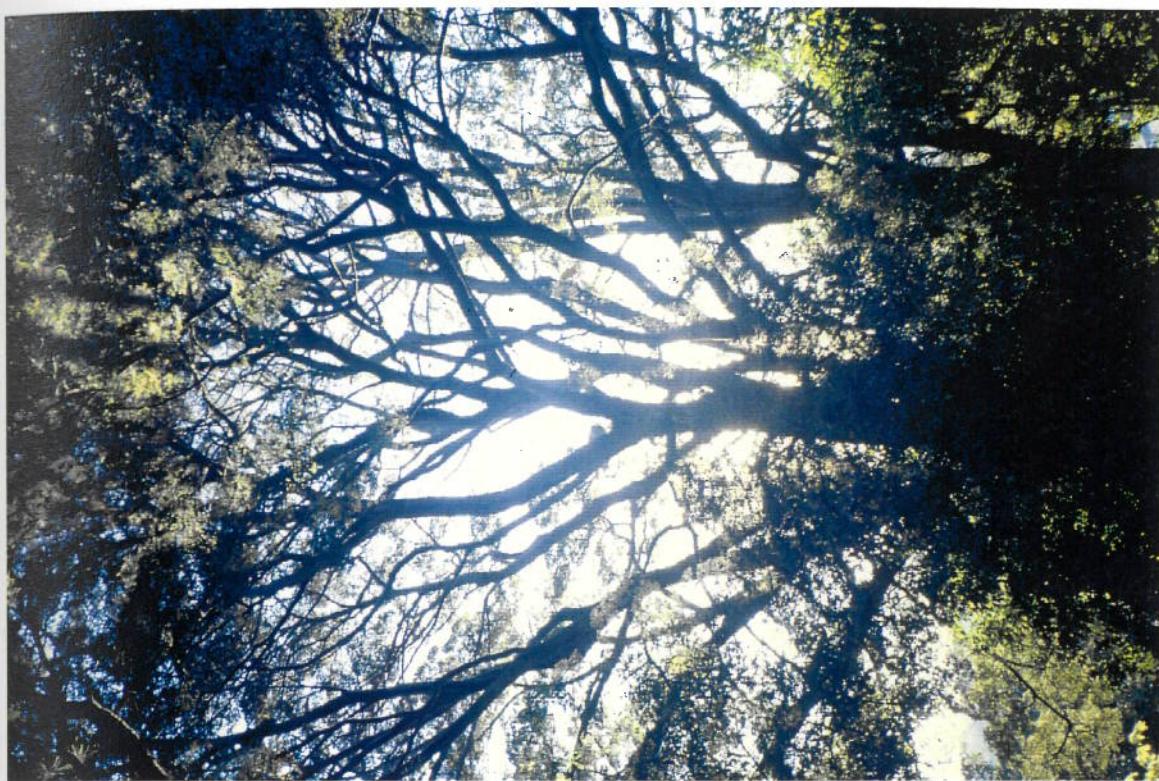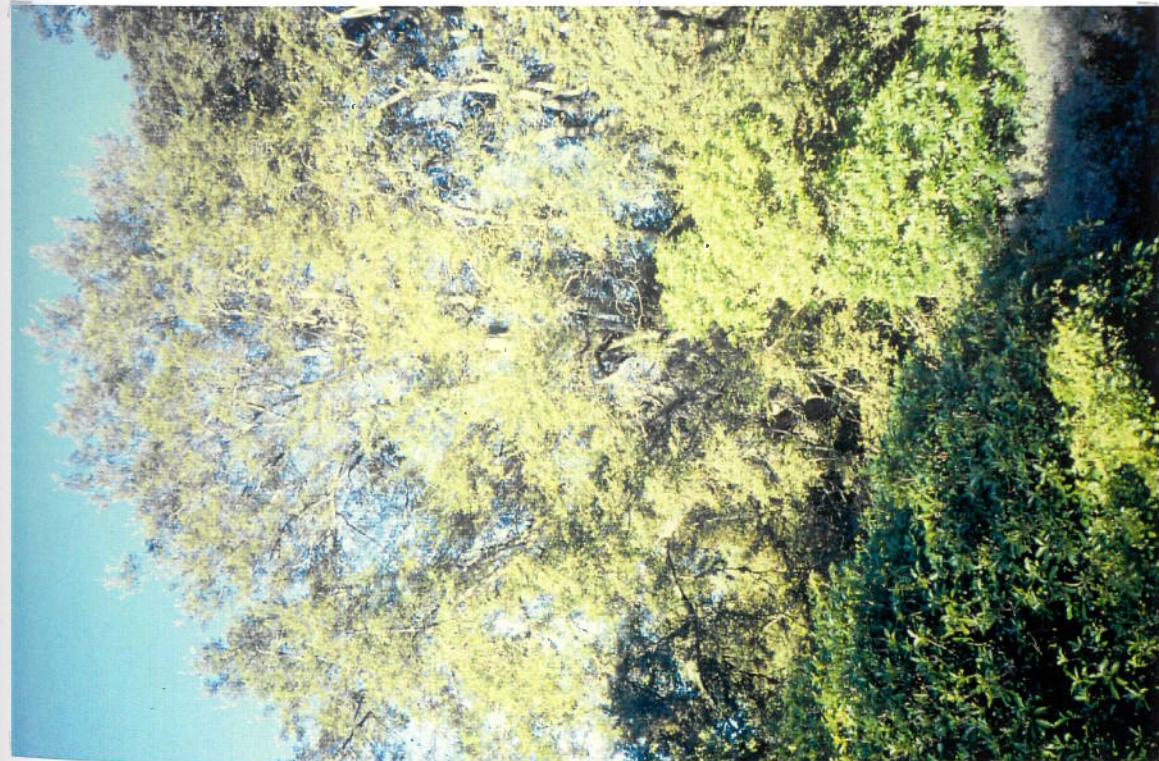
1) *Nothofagus truncata*

2) *Sophora microphylla*
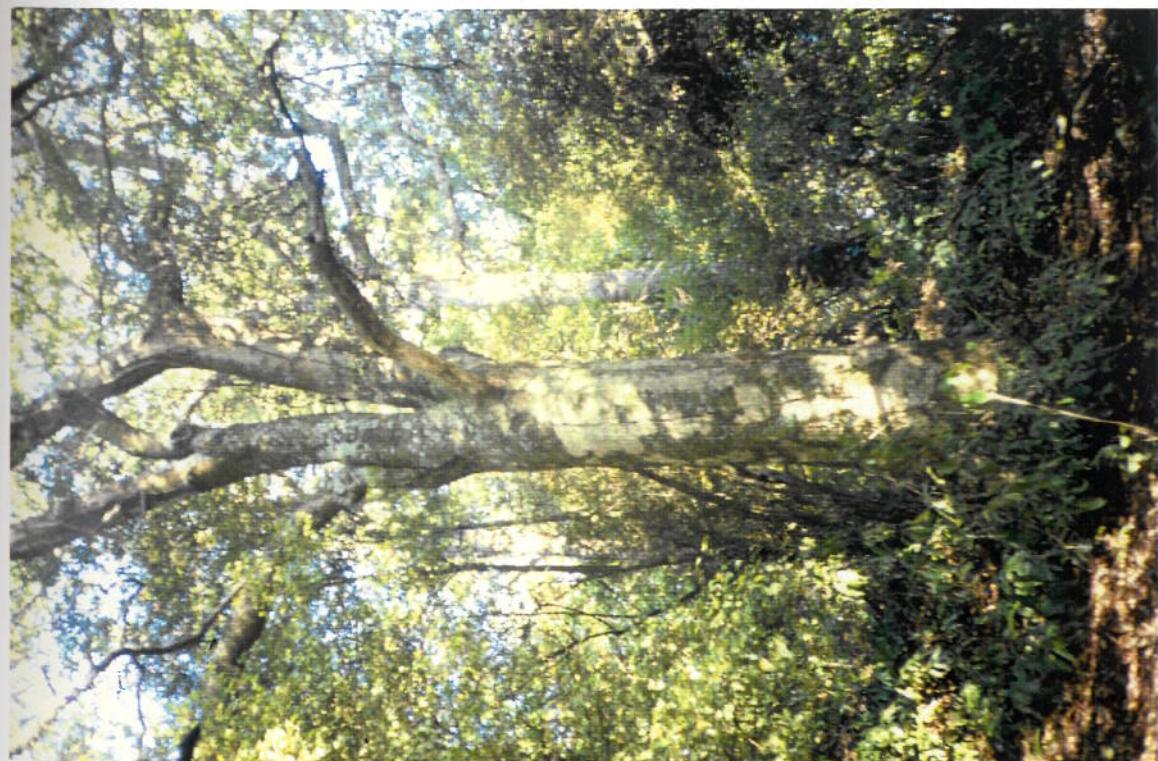
Figure 2.2 c.

1) *Plagianthus regius*

Figure 2.2 d.

2) *Fuchsia excorticata*

1) *Kunzea ericoides*

2.2.2.2 The Town Belt survey area.

Most of the original indigenous vegetation was destroyed in the gold rush times between 1857 and 1864. Subsequently several initiatives by the citizens of Dunedin preserved the green Town Belt. A "trees of the Empire" planting in 1877 heightened interest in the Town Belt and subsequent Arbour day planting bees of various groups and societies established many of the exotic trees (Thomson, 1990).

Sites in the southern Town Belt provided all the exotic deciduous trees, one indigenous tree and one exotic australian tree, namely *Acacia melanoxylon*.

The exotic deciduous trees are *Acer pseudoplatanus, Aesculus hippocastanum, Fagus sylvatica, Fraxinus excelsior, Quercus canariensis, Quercus robur, Quercus rubra, Tilia x europaea, Ulmus procera, Ulmus x hollandica* (Stace, 1991).

Figure 2.2 e

2) *Fagus sylvatica*
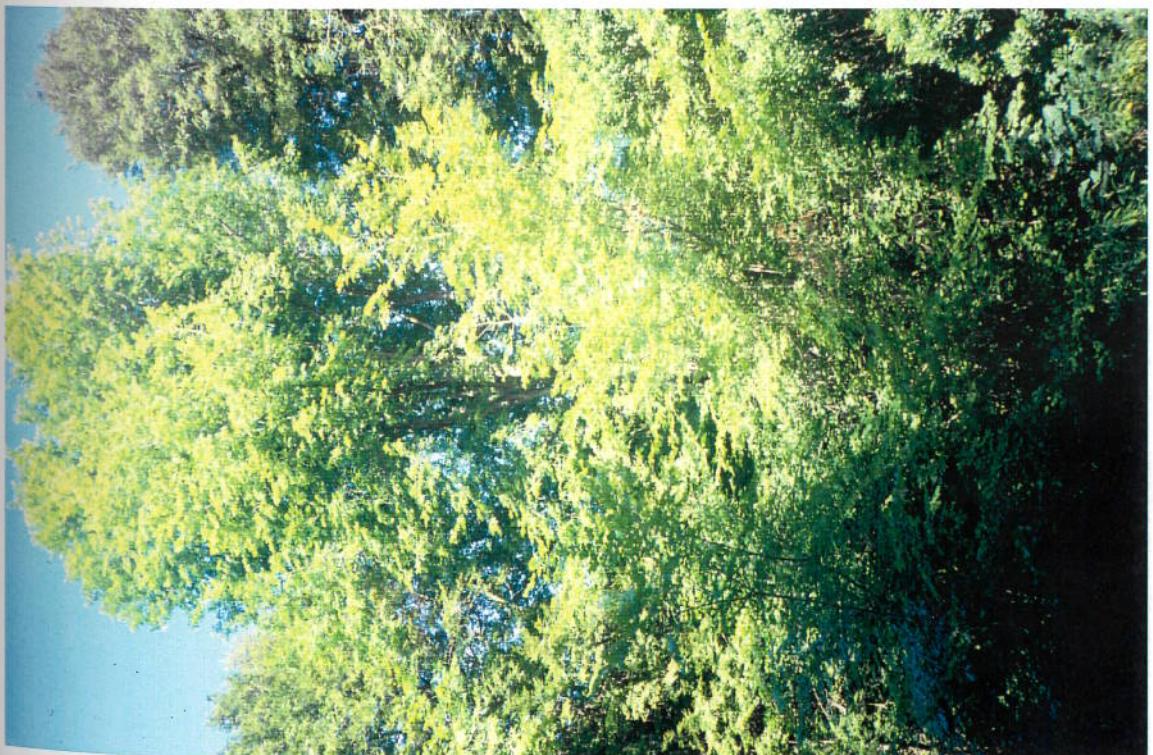
1) *Ulmus procera*
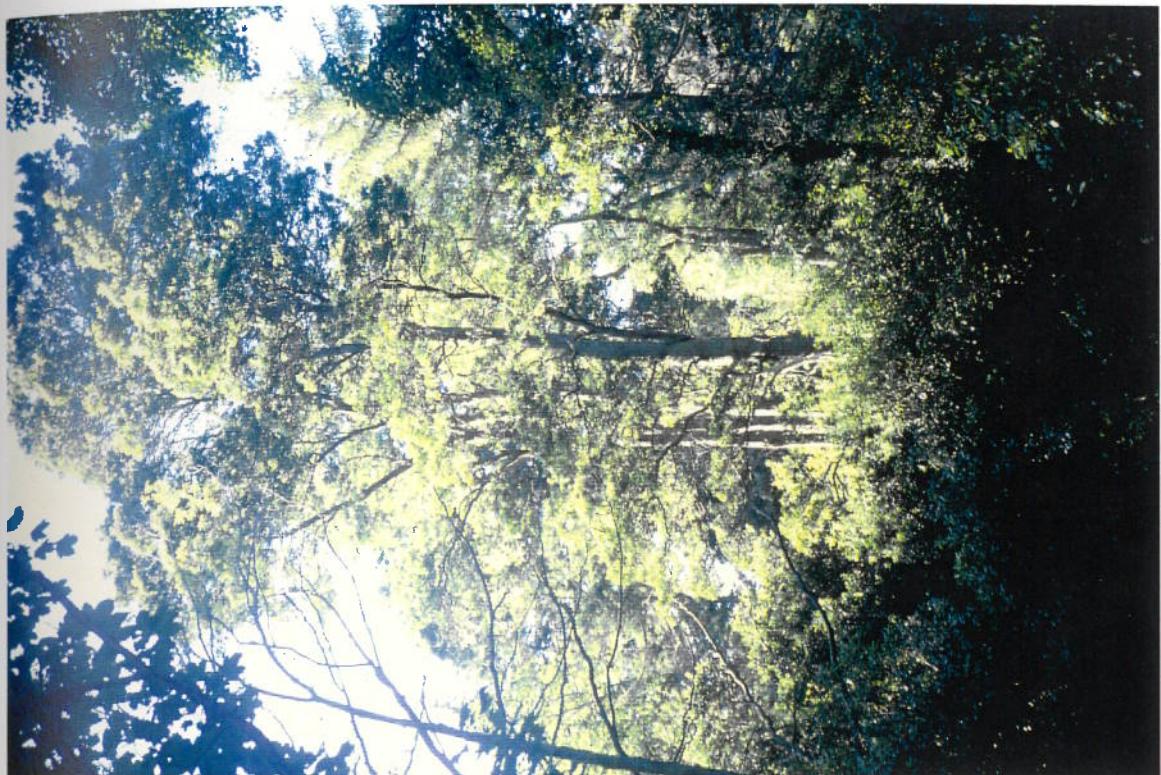
2) *Acacia melanoxylon*

1) *Quercus canariensis*

Figure 2.2 f

2.2.2.3 The Orokonui survey area.

A *Eucalyptus regnans* forest had established as a result of a forest fire in 1906-1907. The seedlings derived from an earlier planting in the 1860's, around the fringe of a later neglected paddock (Simmonds, 1927).

Three *Eucalyptus regnans* were located in the Orokonui survey area. The sampling procedure, as described in section 2.3.1, positioned points for vegetation sampling quadrats and three tree sites from which nine soil samples were taken.

Figure 2.2 g

2) *Eucalyptus regnans* (site 2 western slope)

1) *Eucalyptus regnans* (site 1 near creek)

2.2.2.4 The Flagstaff survey area.

The silver stream drains the western flanks of Flagstaff hill and constitutes an important source of water for the Dunedin city. Fires, ignited by humans, had cleared most of the indigenous cover. Extensive trial plantings of exotic gymnosperms were established from 1909, primarily as a measure of protection against eroding hill sides. The located species include *Cryptomeria japonica*, *Larix decidua*, three *Pinus radiata* and *Pseudotsuga menziesii*. Lately the plantations have become a commercial enterprise of the Dunedin City Council.

Figure 2.2 h

2) **Pseudotsuga menziesii**

1) **Cryptomeria japonica**

Figure 2.2 I

Pinus radiata, 1920, Flagstaff.

Larix decidua, Flagstaff.

Figure 2.2 j

2) Pinus radiata 1965

1) Pinus radiata 1962

Figure 2.2. k Clear-felled sample sites in foreground

2.2.3   Description of trees and sites.

Thirty individual trees were randomly located and three stratified soil samples were collected from each tree.

Ten indigenous trees were located in three survey areas (Mt Cargill, Opoho, Town Belt);

ten exotic deciduous trees were located in the Town Belt survey area.

Four sites had exotic australian trees as a canopy, three of which, with *Eucalyptus regnans*, were located in the Orokonui survey area, and one with *Acacia melanoxylon* in the Town Belt.

Six sampling sites were established nearest to the positions of the quadrats under a coniferous forest canopy at the Flagstaff survey area.

Two additional sites were located in the Flagstaff area, that had recently been clearfelled.

Of the six tree sampling sites, four tree species represent the originally planted varieties. These are *Cryptomeria japonica; Larix decidua; Pinus radiata; Pseudotsuga menziesii.*

Further soil samples were taken from under two second rotation *Pinus radiata*. One was planted in 1962, following a first plantation of *Pinus nigra* and *Picea sitchensis* in 1920. The other site had been planted in 1966, following a mixed *Pinus radiata, Pseudotsuga menziesii* plantation, initiated in 1920.

The location of sample coordinates in the survey area at Flagstaff provided the opportunity to include two sites that had been subjected to recent clearfelling operations. One site was planted in 1920 with *Pseudotsuga menziesii* and clearfelled in 1991. The other site was planted in 1918 with *Pinus radiata* and *Pinus nigra* and clearfelled in March 1993 (Ref. MapDunedin City Council, 1987).

Both sites showed clear signs of impeded water movement down through the A - horizon. This observation supports Leslie's and Tomlinson's (1977) suggestion that forest clearance encourages a process of gleying on these loessial soils.

Random points located one soil sample site in the Town Belt near a *Cupressus macrocarpa* tree next to a road. Subsequent soil analyses showed that roadworks, such as the cutting of a bank and the deposition of material on the downhill side (the site of the trees) had disturbed the loess stratigraphy and let to the inclusion of basaltic

parent material in the soil substrate. Consequently, no further analyses of these three soil samples were made.

This reduced the original number of soil samples form 99 to 96. The 96 soil samples represent the three depth levels from 32 sites, which include two clearfelled sites and thirty individual trees.

The analyses of soil parameters, ordinations and cluster analysis (**chapter 6**) led to the identification of three groupings of trees, which were considered representative of three "forest types".

> indigenous lowland forest (10 replicates);
>
> exotic deciduous lowland forest (10 replicates); and
>
> exotic pyrophyte forest (10 replicates).

The following table 2.1 illustrates data, gathered on breast height diameter, site aspect and slope. The slopes of the sites ranged between 2° and 18°, representing an undulating landscape. Waterlogging was not aparent at any of the forested sites, due to interception and the possibility of surface run from all sites. The aspects ranged widely and is regarded as an important parameter in open landscapes such as grasslands and fields with regard to plant establishment and soil genesis. However, the microclimate under forest cover is generally equitable with regard to temperature, light and moisture fluctuations and aspect is therefore regarded as having a negligible influence on soil properties.

Table 2.1: Environmental Aspects and Tree Diameter

Survey area Opoho Elevation 70 - 80 m.	Breast Height Diameter m	Aspect	Slope
Kunzea ericoides	0.32	220	7
Nothofagus fusca	0.72	328	6
Nothofagus solandri	0.89	290	4
Nothofagus truncata	0.83	160	7
Plagianthus regius	0.45	318	12
Sophora microphylla	0.57	120	5

Survey area Mt. Cargill Elevation 310 - 325 m	Breast Height Diameter m	Aspect	Slope
Dacrydium cupressinum	1.08	100	12
Prumnopitys ferruginea	0.96	108	6
Prumnopitys taxifolia	1.18	88	4

Survey area Town Belt Elevation 60 - 120 m	Breast Height Diameter m	Aspect	Slope
Acacia melanoxylon	0.7	130	5
Acer pseudoplatanus	0.64	240	18
Aesculus hippocastanum	0.43	20	15
Fagus sylvatica	0.86	12	10
Fraxinus excelsior	0.64	65	3
Fuchsia excorticata	0.64	140	9
Quercus canariensis	1.05	90	6
Quercus robur	0.76	25	9
Quercus rubra	0.46	46	11
Tilia europaea	0.43	70	5
Ulmus procera	0.8	120	13
Ulmus x hollandica	0.45	50	8

Survey area Orokonui Elevation 60 - 100 m	Breast Height Diameter m	Aspect	Slope
Eucalyptus regnans	0.96	25	8
Eucalyptus regnans	0.8	60	5
Eucalyptus regnans	1.21	270	4

Survey area Flagstaff Elevation 160 - 240 m	Breast Height Diameter m	Aspect	Slope
Cryptomeria japonica 1920	0.46	100	14
Larix decidua 1918	0.38	330	10
Pinus radiata 1920	1	335	10
Pseudotsuga menziesii 1918	0.67	20	2
Second rotation sites			
Pinus radiata 1962	0.5	210	2
Pinus radiata 1966	0.4	290	2
Clearfelled sites			
Pinus radiata 1993		230	10
Pseudotsuga menziesii 1991		80	4

3.   Analysis of Sample Quadrats and Community Structure

Introduction

This chapter compares the sub-canopy vegetation at, or close by the canopy trees from where stratified soil samples were taken. Abundance and height of all higher plant species was noted in the field and subsequently statistically analysed. A detailed species list of the sample quadrats is given in the Appendix: B; Table 1.

Quadrats were established at the two clearfelled sites in Flagstaff, to obtain positions in the field for soil sampling. Vegetation was completely lacking at one site and ruderals, Cyperaceae and Gramineae sparsely covered the other site. The recent site disturbances and the lack of a canopy meant that the sites could not be compared with the other sites. The vegetation was therefore not surveyed at the clearfelled sites.

3.1 Methods

The field notes on species abundance and height estimates were classified according to Raunkiaer's (1922) life form classification system. A letter denotes the heightclass of a particular species in the quadrat.

A; for a megaphanerophyte of > 30 m height.

B; for a mesophanerophyte of 8 - 30 m height.

C; for a microphanerophyte of 2 - 8 m height.

D; for a nanophanerophyte of 0.4 - 2 m height.

E; for seedling trees and herbs and others of < 0.4 m height.

The numbers behind the letters denote the frequencies of occurrence of a species in the particular height class in a sample quadrat.

The number of species in the "seedlings" row refers to the tree species number in the "E" size class, and was usually of very high abundance.

The number of species within each quadrat was noted and a ratio calculated for the mean species density; Σ abundance / Σ species.

The results are summarized in table 3.1.

3.2 Results.

The vegetation composition of the sample quadrats:

Table 3.1 Vegetation classification of quadrats

Abundance	1 Mt.Cargill	2 Mt.Cargill	3 Townbelt	4 Opoho	5 Opoho	6 Opoho	7 Opoho
Sizeclass	Dacrydium cu.	Prumnopitys ta.	Fuchsia ex.	Kunzea er.	Nothofagus fu.	Nothofagus tr.	Plagianthus re.
> 30 m							
8 - 30 m	1	1		3	2	1	2
2 - 8 m	22	27	6	11	9	6	8
0.4 - 2 m	41	41	6	19	6	6	12
< 0.4 m	1	1			2		
Total	65	70	12	33	19	13	22
Seedlings~		2 species	1 species	3 species	1 species	1 species	3 species
Species	19	24	6	16	12	9	15
Abd. / spec.	3.4	2.9	2.0	2.1	1.6	1.4	1.5

Abundance	8 Opoho	9 Townbelt	10 Townbelt	11 Townbelt	12 Townbelt	13 Townbelt	14 Townbelt
Sizeclass	Sophora mi.	Acer ps.	Aesculus hi.	Fagus sy.	Fraxinus ex.	Quercus ca.	Quercus ro.
> 30 m							
8 - 30 m	3	2	1	4		1	1
2 - 8 m	9	10	5	19	36	8	14
0.4 - 2 m	11	21	11	36	41	6	28
< 0.4 m		9	3	6	14		12
Total	23	42	20	65	91	15	55
Seedlings~	2 species		1 species		1 species	1 species	
Species	13	14	17	15	16	10	15
Abd. / spec.	1.8	3.0	1.2	4.3	5.7	1.5	3.7

Abundance	15 Townbelt	16 Townbelt	17 Townbelt	18 Townbelt	19 Flagstaff	20 Flagstaff	21 Flagstaff
Sizeclass	Quercus ru.	Tilia eu.	Ulmus pr.	Ulmus ho.	Cryptomeria ja.	Larix de.	Pinus ra.
> 30 m							
8 - 30 m	2	1	3	5	7	3	1
2 - 8 m	18	2	18	11		2	
0.4 - 2 m	42	69	24	30	8	8	4
< 0.4 m			1	4		1	10
Total	62	72	46	50	15	14	15
Seedlings~	1 species	1 species	1 species	1 species	1 species	2 species	
Species	14	10	18	16	7	9	5
Abd. / spec.	4.4	7.2	2.6	3.1	2.1	1.6	3.0

Abundance	22 Flagstaff	23 Flagstaff	24 Flagstaff	25 Townbelt	26 Oroconui (creek)	27 Oroconui	28 Oroconui
Sizeclass	Pinus ra.	Pinus ra.	Pseudotsuga me.	Acacia me.	Eucalyptus re.	Eucalyptus re.	Eucalyptus re.
> 30 m			2			1	1
8 - 30 m	2	2		3			3
2 - 8 m	1	1		31	35	6	6
0.4 - 2 m	13	12	21	24	26	6	5
< 0.4 m	3	18	20	3	7	7	14
Total	19	33	43	61	68	20	29
Seedlings~				4 species		1 species	
Species	5	9	12	15	22	8	8
Abd. / spec.	3.8	3.7	3.6	4.1	3.1	2.5	3.6

3.2.1 Overview.

The table 3.1 documents clear differences in the abundance and height distribution of subcanopy plants near particular canopy species.

The highest vegetative abundances and species diversities were found near the podocarps in the old growth forest and at a *Eucalyptus regnans* site next to the Orokonui creek.

High subcanopy abundance and diversity values were found near exotic deciduous trees, in particular *Fraxinus excelsior, Tilia x europaea, Fagus sylvatica, Quercus rubra and Q. robur, Ulmus x hollandica* and *U. procera*, as well as *Acacia melanoxylon* and *Pseudotsuga menziesii*. However, in the *Pseudotsuga menziesii* quadrat the growth of subcanopy species is restricted to the lower height classes of 0 - 2 m height.

The species diversity near the indigenous trees from the Opoha area was often similar to that of the exotic deciduous trees, but lower abundances were recorded.

Lower abundances and subcanopy species diversities were also noted under *Eucalyptus regnans* forest, away from the immediate area of the creek, in the old *Pinus radiata* forest (1920), and under *Fuchsia excorticata, Nothofagus truncata, Larix decidua, Pinus radiata, Cryptomeria japonica* and *Quercus canariensis*.

3.2.2 Suggested explanations for observed differences.

The relatively undisturbed indigenous forest at Mt. Cargill had the highest diversity and density of species.

These sites provide a useful regional base line with other sites.

The average abundance in the Mt. Cargill quadrats was 68 and the mean species diversity was 22.

The ratio of mean species density diversity is indicated as ranging between 2.9 to 3.4 and the ratio of the height classes "D" 0.4 - 2 m to "C" 2 m - 8 m ranges around 1.5 to 1.9 respectively.

At the Opoho site, a high species diversity was found near the deciduous *Plagianthus regius*. The *Kunzea ericoides* forest showed high diversity and abundance of species, as can be expected for an early successional canopy species. Comparatively low abundances of subcanopy species near indigenous canopy trees were generally noted in the Opoho area. This can possibly in part be explained by the location of sites in the botanic garden reserve. At the time of sampling there were no visible signs of management, but, areas in the vicinity of the sites were weeded during the following year.

Consequently, past weeding activities could be partly responsible for the comparatively low abundance of subcanopy species.

The quadrat under *Fuchsia excorticata* forest showed lowest abundance and species diversity. Neither water, light nor soil quality (see chapter 6) of the site could possibly limit subcanopy species diversity. One possible reason might be impeded cold air drainage, since the site was located near the base of a steep-sided creek channel.

The wide range of values for subcanopy abundance and diversity in the samples, associated with the indigenous canopy vegetation is therefore possobly a consequence of both, limitations to the subcanopy, caused by physical site characteristics (*Fuchsia excorticata*) or light availability (*Nothofagus*) and favourable effects of shelter and complementary nutrient cycling (Stevenson, 1982; 1986) between canopy and subcanopy species.

Abundances ranged between 12 and 70, with an average of 20 being most frequent in the Opoho site (compared to an average of 68 for the Mt. Cargill indigenous forest).

Species diversities ranged between 6 and 24, with an average of 12 in Opoho (and 22 at Mt. Cargill).

The species abundance and diversity was relatively high near most deciduous trees, except *Fuchsia excorticata*. The light availability during winter and early spring is an obvious bonus to indigenous subcanopy species, adapted to limited light availabilities throughout the year. The abundance of indigenous subcanopy plants was particularly interesting in the stands of *Fagus sylvatica*, which, in their region of origin, on an equivalent acidic pedon, and due to the effective utilization of light during the summer months, are typically devoid of subcanopy plants.

Subcanopy species abundances ranged between 15 and 91. The most frequent abundances were near the average of 52.

Species diversities ranged between 10 and 18, with a median of 15 in the sample quadrats of the deciduous forest.

The mean species density is variable and ranges between 1.2 to 7.2 and most commonly averages around three to four specimen per species per sample quadrat.

The highest abundances were commonly found in the 0.4 - 2 m height class, which had a common ratio of 1.8 to the 2 m - 8 m height class. One exception was the site near *Quercus canariensis*, which has a dense crown and persistent leaves throughout winter.

The abundance and species diversity seems to be related primarily to the availability of light, water and soil nutrient availability.

This is demonstrated clearly in the differences of the sites under *Eucalyptus regnans*. Light is not a limiting factor for most subcanopy species in this stand. Water and nutrient availability however are limiting factors for subcanopy growth, particularly with distance from the creek.

The *Eucalyptus* site (1) near the creek had little water or light limitations, hence the subcanopy was luxuriant, both in abundance and diversity and comparable to the podocarp forest. However, a short distance uphill either side of the creek, water and nutrients rapidly become limiting factors for subcanopy growth, due to the extraction efficiency of the eucalypts (see chapter 6 and Appendix: A; 2.5) and abundances and diversity levels fall to the amounts, typical for the Pinaceae.

The subcanopy near *Acacia melanoxylon* is rich in adundance and species composition and quite similar in appearence to the eucalypt forest near the creek.

A striking feature of all Pinatae (Cryptomeria and Pinaceae) forests is the restriction of the subcanopy to lower height classes than in the other forests. The "C" height class of 2 to 8 m is practically absent in the conifer forests. Specimens in the "E" height class (0 - 0.4 m) predominate in the old growth *Pseudotsuga menziesii* and *Pinus radiata* forests. Nuances of combinations of limiting factors explain some individual site differences. The absence of subcanopy species in the "C" height class in the *Cryptomeria japonica* forest and the absence of the "C & B" height class in *Pseudotsuga menziesii* forest can partly be attributed to light limitations, water limitations caused by interception and nutrient limitations (see chapter 6). In the *Larix decidua* forest, where the soil nutrient status is the only limiting factor a few specimens of all height classes are found. In the *Pinus radiata* forests of various ages, the low height classes, abundances and species diversities are a result of severely limiting conditions for growth. The limiting conditions include, a soil nutrient status within the toxicity range of the Al - Fe buffer capacity (refer to results and discussions in chapters 6 and 8), water limitations due to interception losses of the living pine trees and the mor organic layer and limited light availabilities, particularly at times of low solar angle.

3.2.3 Cluster analysis.

3.2.3.1 Methods.

The data was subjected to a cluster analysis, using the unweighted pair-group method and the Jaccard coefficient.

The formula is: $SJ = a / a + b + c$;

where SJ = Jaccard similarity coefficient;

a = number of species common to all quadrats

b = number of species in quadrat 1

c = number of species in quadrat 2

Dissimilarity is then: $DJ = b + c / a + b + c$; or $1.0 - SJ$.

The similarity of quadrats could thus be assessed in terms of species composition.

Florasurvey

Dendrogram of vegetation quadrats

Figure 3.1

Da.cu.
Pr.ta.
Eu.re.1
Eu.re.2
Eu.re.3
Cr.ja.
La.de.
Pi.ra.1965
Pi.ra.1962
Pi.ra.1920
Ps.me.
Fu.ex.
Ku.er.
No.fu.
Pl.re.
So.mi.
No.tr.
Ac.ps.
Ae.hi.
Fr.ex.
Qu.ca.
Qu.ro.
Qu.ru.
Ti.eu.
Ac.me.
Ul.ho.
Fa.sy.
Ul.pr.
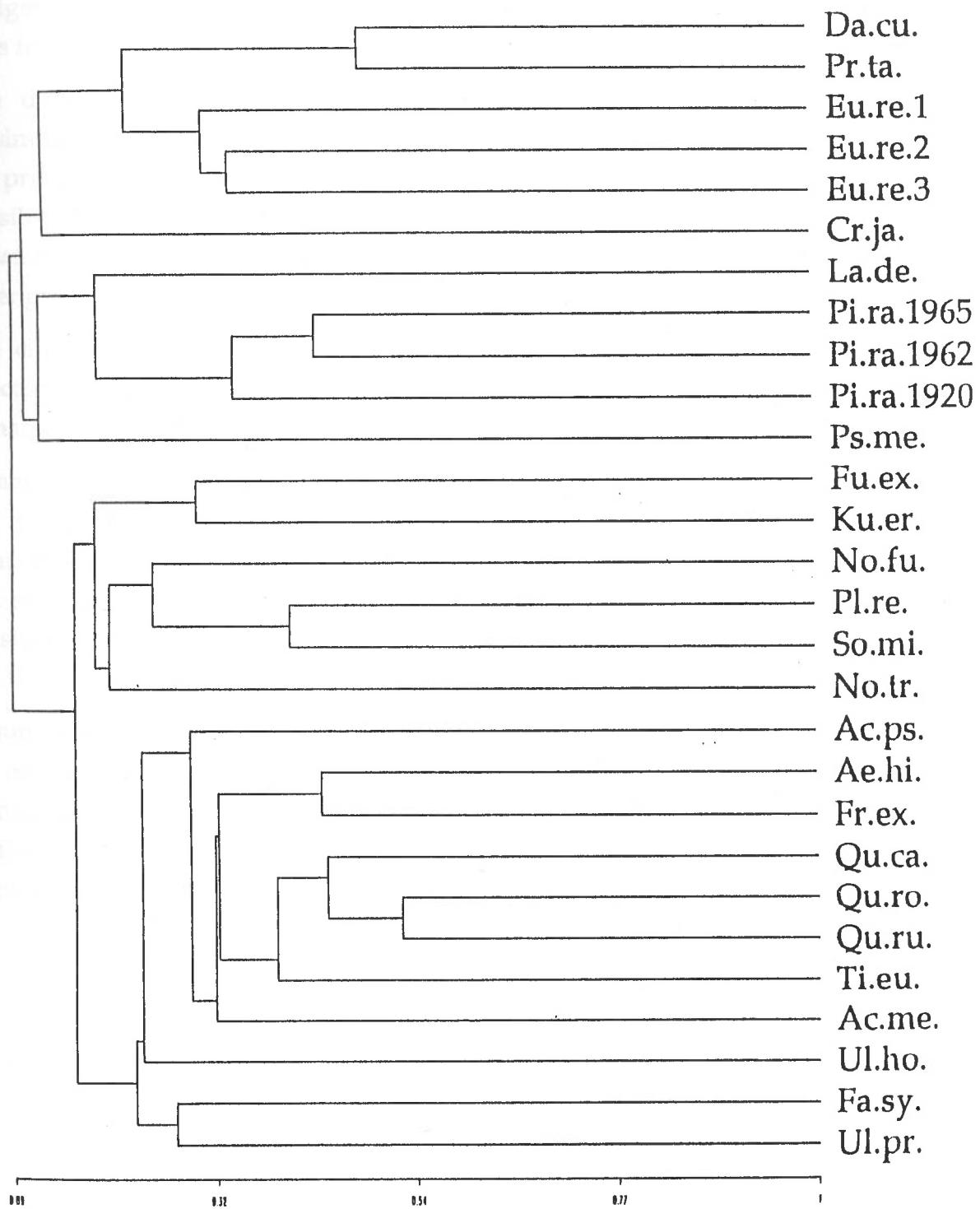
The closest floristic relationships are found between sites that are in close proximity with similar canopy trees. The samples from the deciduous Town Belt site are grouped together, as expected. The Opoho site with indigenous canopy trees is grouped together and joined by *Fuchsia excorticata* from the Town Belt, which is floristically related to the *Kunzea ericoides* site.

The similarities between the latter pair and the two *Nothofagus* quadrats to the other indigenous trees in the Opoho area is not much less than the similarities between sites in the Town Belt area.

The dissimilarities between other survey sites are rather large. The floristic dissimilarities between Flagstaff and Orokonui are larger than differences between the previous survey sites. The Mt. Cargill and Orokonui sites show some affinity, possibly due to the one floristically rich eucalypt forest site near the creek. *Pseudotsuga menziesii* and *Cryptomeria japonica* sites are floristically dissimilar to most other groups.

The cluster analysis indicates that the subcanopy species composition might be affected by the location, the effect of the canopy species and the history of management practices, since the establishment of the canopy tree species.

Management practices are unlikely to have influenced the species compositions at the indigenous Mt Cargill area, they are likely to have influenced the species composition of the indigenous Opoho area and possibly the exotic deciduous Town Belt area. Management practices, influencing species compositions are less likely at the sites of the eucalypts in Orokonui and the old growth gymnosperms in Flagstaff and they are certain at the second rotation sites of gymnosperms in Flagstaff.

In summary, the location of post-clearance indigenous subcanopy species refugia, the migrating capabilities of species, the biological influence of the area specific canopy flora, variations in site management, might all contribute to the (dis)-similarities between sites or locations with regard to species diversity. An attempt to discuss the significance of various influences is therefore speculative at this stage.

4   Soil Sampling Methods and

Description of the Sites' Litter Layers.

Introduction

This chapter describes the field methods used to collect soil A-horizon - and sub-soil samples. Figures 4.1 and 4.2 show the results of the sub-soil pH values and the particle size analysis of all survey areas.

The organic litter layers of the soil sample sites are described in paragraph 4.3 and illustrated in table 4.1.

4.1   Description of soil sampling methods.

The sampling of the three soil A - horizon strata was completed within a few days in late summer (16. - 21. 3. 93). Settled weather conditions, with no rain and overcast skies, prevailed throughout the period of soil sampling.

The organic-mineral horizon at the sample sites was usually 16 - 18 cm deep.

Three depths from the A - horizon were sampled, to provide some indication of nutrient cycling by the primary producers.

Four soil samples were taken from under each of the trees of the five survey areas.

All four samples were taken at the same distance from each other and at points, that were half way between the trunk and the drip-line of each tree.

The sampling position between the tree trunk and the drip-line was considered to best represent the influence of the tree upon the soil and also avoided potential distortions of the soil-chemistry near the trunk, caused by precipitation and deposition of leached nutrients (Walter, Breckle, 1985; Stevenson, 1985).

Each of the four samples contained stratified subsamples at three set depths within the soil A - horizon. The four samples were subsequently pooled, using a soil sample splitter, to obtain, for each tree, three distinct soil samples from three depths: from the top of the mineral A - horizon (= zero) to 1 cm; from 7 - 8 cm; from 14 - 15 cm.

The top of the A- horizon was taken as 0 cm, so that comparable samples could be obtained from different sites. Variations in the thickness of the litter- and semi-decomposed organic layers, necessitated this determination.

The top of the A - horizon was determined by the first occurrence of mineral matter that would not be moved with a fine brush. A spade was used to obtain a vertical soil profile, which was marked at 7 cm and at 14 cm. A sample of 1 cm thickness was taken from the top. The top soil down to 7 cm was removed and another sample of 1 cm thickness was taken. The next layer of top soil (8 - 14 cm) was put aside and the third soil sample was taken at a depth of 14 - 15 cm.

The soil samples form the basis for a comparative analysis of the trees influence on the soil medium.

At the clearfelled sites, the three soil depth samples were obtained by combining four samples of equivalent depths per site, in the same way as described above. The four samples per site were established to the north east of the randomly selected points in the field at the four corners of the 5 x 5 m quadrat.

Figure: 4

Illustration of the soil sampling method.
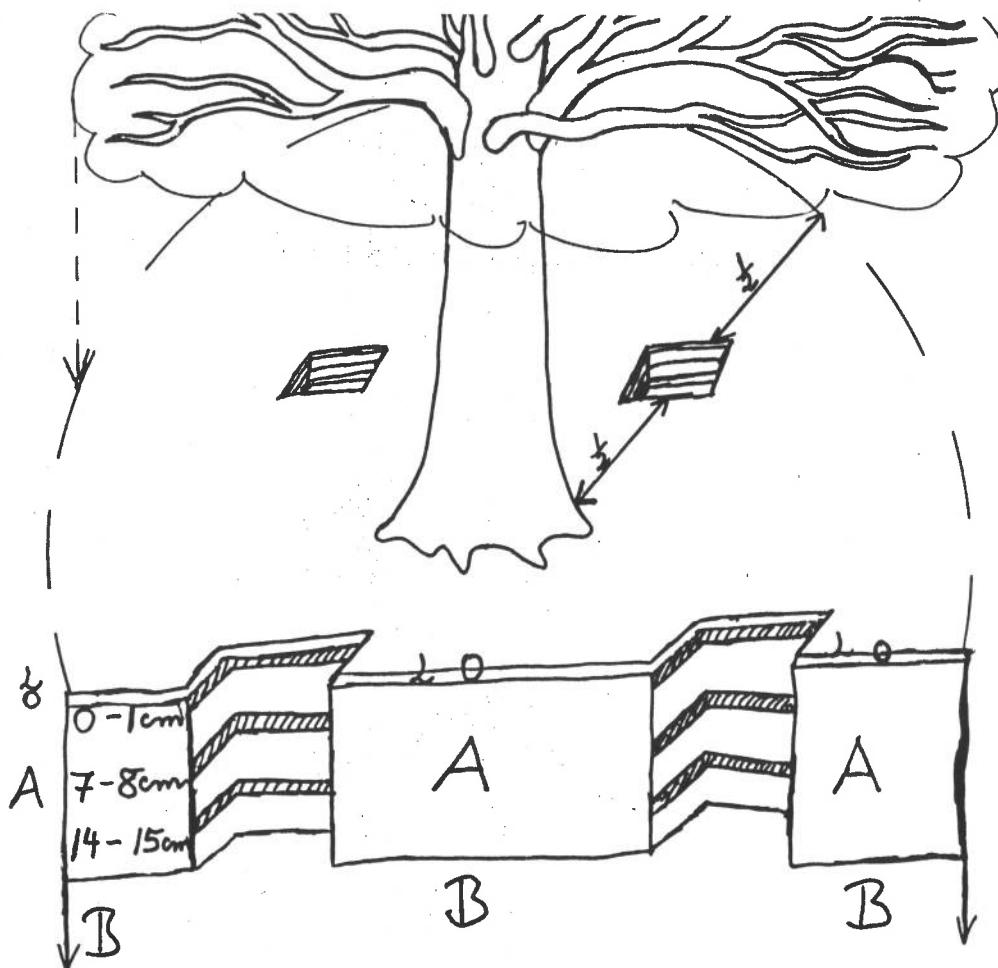
Variations in the organic layers are described in section 4.3

4.2 The soil B-horizon.

4.2.1 Methods.

Soil B- horizon samples were collected concurrently from each survey area. In all cases the randomly assessed locations for soil A - horizon sampling sites were taken. One out of three sample sites at the Mt. Cargill survey area was randomly chosen to locate a sub-soil sampling site.

A road cut was used to describe the sub-soil and to obtain a sample at the Opoho survey site

Three sub-soil samples were randomly chosen from the 12 soil A - horizon sample sites in the Town Belt area.

Two sites each were randomly identified for sub-soil sampling at the Orokonui and Flagstaff survey areas.

As the sub-soil samples were collected, care was taken to minimize disturbances to the vegetation and to return the excavated soil in its original stratified condition. The excavations were carried out to a depth of one metre and composite soil samples were taken from thirty to one hundred centimetres depth. Analyses for each site included the measuring of pH values and a particle size analysis.

The soil B - horizon sample sites will be described as they occur adjacent to various trees and in conjunction with the description of the organic layers under all sample trees.

4.2.2 Results

The results support the assumption that four survey sites (Opoho; Town Belt; Flagstaff and Orokonui) have a common loessial substrate, as suggested by the research results of Tomlinson and Leslie (1977).

The Mt. Cargill site is slightly different. The sand fraction at Mt. Cargill is higher and the pH lower, as might be expected from the higher precipitation and steeper relief at this site.

Figure 4.1

Soil B- horizon pH
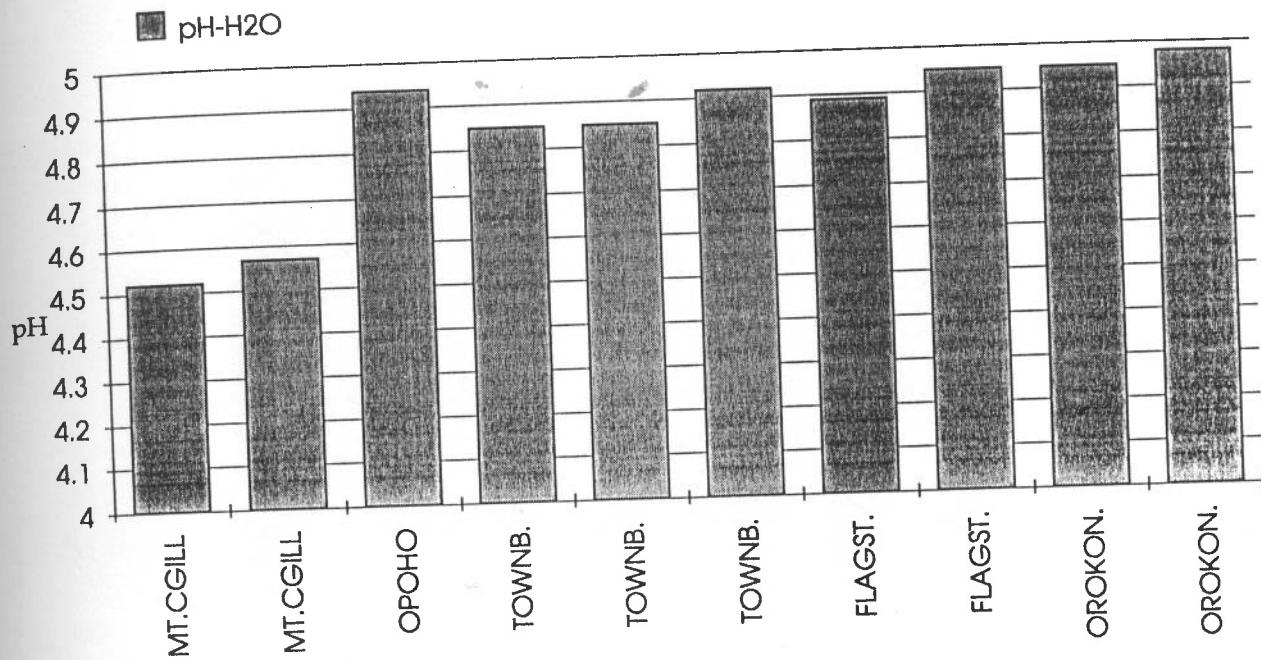
Figure 4.2

Particle Size Analysis
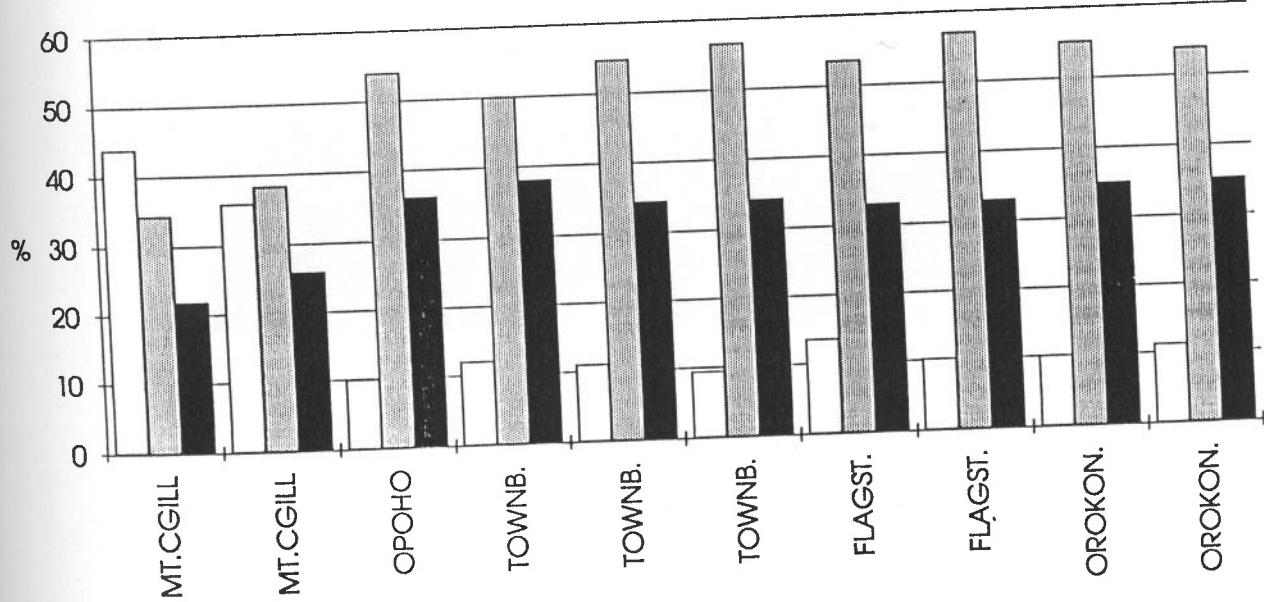
Figure 4.3. a   Soil sample site Town Belt, near *Fagus, Ulmus*.

Figure 4.3. b Soil sample site Town Belt, near *Fagus, Quercus, Fraxinus.*
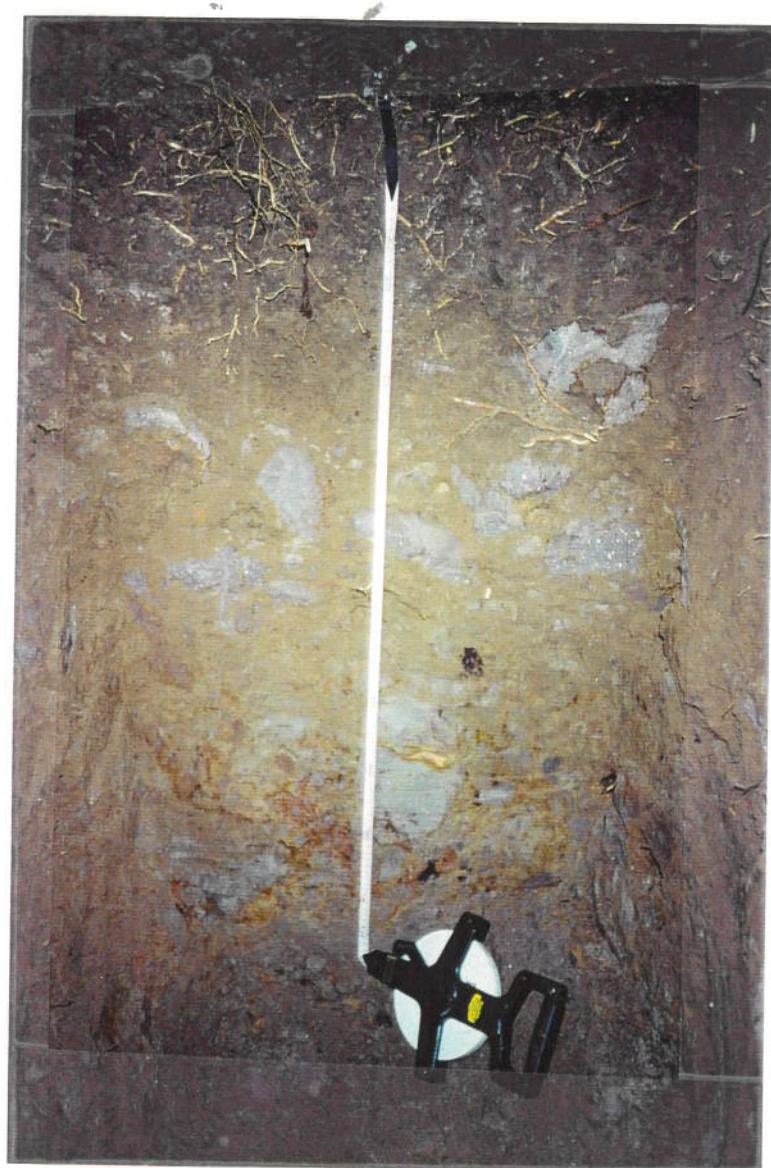
**Figure: 4.3 c   Soil sampling site, Mount Cargill;
weathered phonolite in loess matrix.**

Figure: 4.3 d   Soil sampling site, Orokonui, in *Eucalyptus regnans* forest

Figure: 4.3 e   Soil sampling site, Flagstaff, in *Pseudotsuga menziesii* forest.

Figure: 4.3 f Soil sampling site, Flagstaff, in *Pinus radiata* forest.

4.3   Description of the organic layers and the soil horizons at sample sites.

The table 4.1 illustrates the composition and stratification of the organic litter layers under the individual trees.

The following average measurements, derived from four sub-samples, on the organic layers L, O_f and O_h and were made at the tree sites, which had soils samples taken. The litter and the organic layers were sampled and described in early summer (21st. of December 1994).

Specific observations concerning the litter layers, as well as portraits of the soil horizons, wherever applicable are outlined in paragraph 4.3.1.

The stratification of the litter layer.

L   : (undecomposed litter);
O_f :(organic horizon with fermented, partly decomposed organic substance);
O_h :(organic horizon with humified, largely decomposed organic substance),(Schroeder,1984).

Table 4.1: The stratification of litter layers.

Survey area Opoho	"L" in cm	"O$_f$" in cm	"O$_h$" in cm
Kunzea ericoides	2 to 4	1	n.a.*
Nothofagus fusca	1 to 5	1 to 2	2 to 4
Nothofagus solandri	1.5 to 5.5	1	1 to 3
Nothofagus truncata	2 to 6	1 to 3	1 to 3
Plagianthus regius	2	n.a.	n.a.
Sophora microphylla	1	n.a.	n.a.
Survey area Mt. Cargill	"L" in cm	"O$_f$" in cm	"O$_h$" in cm
Dacrydium cupressinum	3 to 5	1 to 2	1 to 5
Prumnopitys ferruginea	1	2	1 to 4
Prumnopitys taxifolia	2 to 4	3 to 4	1 to 3
Survey area Town Belt	"L" in cm	"O$_f$" in cm	"O$_h$" in cm
Acacia melanoxylon	2 to 6	1	n.a.
Acer pseudoplatanus	2	1	0.5
Aesculus hippocastanum	3	2	1
Fagus sylvatica	2 to 5	1 to 3	1
Fraxinus excelsior	2	n.a.	n.a.
Fuchsia excorticata	1 to 4	n.a.	< 1
Quercus canariensis	3	2	0.5
Quercus robur	2 to 5	1 to 3	0.5
Quercus rubra	1 to 4	1 to 3	0.5
Tilia europaea	1	n.a.	1
Ulmus procera	1	n.a.	1
Ulmus x hollandica	1 to 2	n.a.	1
Survey area Orokonui	"L" in cm	"O$_f$" in cm	"O$_h$" in cm
Eucalyptus regnans	8 to 10	4 to 5	n.a.
Eucalyptus regnans	5 to 7	5 to 7	n.a.
Eucalyptus regnans	7 to 9	4 to 6	n.a.
Survey area Flagstaff	"L" in cm	"O$_f$" in cm	"O$_h$" in cm
Cryptomeria japonica 1920	5 to 13	3 to 7	n.a.
Larix decidua 1918	3 to 7	3 to 7	n.a.
Pinus radiata 1920	4 to 8	8 to 12	n.a.
Pseudotsuga menziesii 1918	1 to 4	2 to 4	n.a.
Second rotation sites			n.a.
Pinus radiata 1962	5 to 11	7 to 10	n.a.
Pinus radiata 1966	4 to 9	5 to 9	n.a.
Clearfelled sites			
Pinus radiata 1993	0 to 150	< 1	n.a.
Pseudotsuga menziesii 1991	0 to 200	< 1	n.a.

n.a.*[1] : not apparent

This table illustrates clearly species specific differences in the litter quality.

4.3.1 Sample sites of indigenous trees.

4.3.1.1 Trees at the Survey area Opoho.

A road cut at Lovelock Ave. provided an opportunity for the assessment of the Opoho soil horizons. The site had a slope of $3°$ and an aspect of $159°$. The soil A - horizon descended to 15 cm and contained 80 % of the visible portion of roots. The soil B-horizon was yellow mottled, down to 60 cm and contained grey bands at depths over 60 cm. The loess cover was greater than 2 m.

Kunzea ericoides: L 2 - 4 cm; O_f 1 cm; O_h n. a.

Nothofagus spp: leaf, seed and woody litter in various stages of decomposition.

Plagianthus regius: L 2 cm of Coprosma and Mahoe leaf litter, all leaves of *Plagianthus regius* were thoroughly decomposed 8 months after abscission and fully integrated into the mineral A - horizon.

Sophora microphylla: L 1 cm of leaf stems, all leaves of *Sophora microphylla* were fully integrated into the mineral A - horizon.

Fuchsia excorticata: L 1 - 4 cm; O_h < 1 cm. Leaves decomposed within 8 months.

4.3.1.2 Trees at the Survey area Mt. Cargill.

Dacrydium cupressinum: L 3 - 5 cm, mainly leaves and bark flakes of *Dacrydium cupressinum*; O_f 1 - 2 cm; O_h 1 - 5 cm.

Prumnopitys ferruginea: L 1 cm, predominantly shed male cones; O_f 2 cm; O_h 1 - 4 cm.

The B - horizon soil sample site was situated about 12 m to the north of the tree in order to avoid potential damage to the tree roots.

An A - horizon, very rich in organic material, reached down to 25 cm and gradually faded into the B - horizon.

Solifluction was evidenced by the weathered phonolite boulders within the loess matrix of the profile. The mixing of the loess matrix with organic material was extensive and reached to 75 cm depth. Orange mottling was frequent at depths of more than 80 cm.

Prumnopitys taxifolia: L 2 - 4 cm, predominantly shed barkflakes; O_f 3 - 4 cm; O_h 1 - 3 cm.

4.3.2   Sample sites of exotic deciduous trees.

4.3.2.1 Trees at the Survey area Town Belt.

Acer pseudoplatanus: L 2 cm, mainly indigenous leaf litter 8 - 9 months after abscission; Of 1 cm, fragments of *Acer pseudoplatanus* leaves; Oh 0.5 cm.

Aesculus hippocastanum: L 3 cm seed, husk and leaf litter of *Aesculus hippocastanum* and indigenous leaves; Of 2 cm; Oh 1 cm.

Fagus sylvatica: L 2 - 5 cm; Of 1 - 3 cm; Oh 1 cm grading into soil A - horizon. The A - horizon grades into the B - horizon at 20 - 30 cm depth.

The B - horizon is characterized by yellow and orange mottles, down to a depth of 60 cm and containing grey vertical lines in a orange - yellow matrix at depths greater than 60 cm.

Fraxinus excelsior: L 2 cm, mainly of indigenous origin (*Coprosma; Melicytus*). The litter of *Fraxinus excelsior* was thoroughly decomposed and integrated into the A - horizon, 8 months after abscission.

Quercus canariensis: L 3 cm; Of 2 cm; Oh 0.5 cm;

soil A horizon 0 - 16 cm;

soil B horizon: uniform pale yellow to 35 cm, interspersed with top soil filled root channels, occasional orange - yellow mottles down to 70 cm, grey bands and orange mottles, within a yellow matrix of loess.

Quercus robur L 2 - 5 cm; Of 1 - 3 cm; Oh 0.5 cm.

Quercus rubra L 1 - 4 cm; Of 1 - 3 cm; Oh 0.5 cm.

Tilia x europaea L 1 cm, leaves from indigenous origins, *Tilia x europaea* leaves were thoroughly decomposed and integrated within 8 months ; Oh 1 cm.

Ulmus procera L 1 cm, leaves from indigenous origins, *Ulmus procera* leaves were thoroughly decomposed and integrated within 8 months ; Oh 1 cm.

Ulmus x hollandica L 1 - 2 cm, leaves from indigenous and Quercus origins, *Ulmus x hollandica* leaves were thoroughly decomposed within 8 months ; Oh 1 cm.

A distinctly black A - horizon reached 15 cm, channels filled with top soil reaching 40 cm depth.

The B - horizon has a yellow hue with increasing orange mottling from 35 cm depth. Grey patches can be seen from 50 cm depth and strong contrasting grey lines in an

orange mottled yellow earth are distinct from 70 cm depth. Live roots penetrate both soil horizons.

4.3.3 Sample sites of exotic australian trees.
Trees at the Survey area Orokonui.

Acacia melanoxylon: L 2 - 6 cm; Of 1 cm. Dry, resistant litter in various stages of decomposition. Depth of soil A - horizon 0 - 17 cm.

Eucalyptus regnans 1: L 8 - 10 cm; Of 4 - 5 cm;

depth of soil A - horizon 0 - 15 cm;

soil B - horizon: 15 - 25 cm yellow brown mottled; 25 - 60 cm yellow grey, mottled orange; 60 - 100 cm yellow - orange with grey vertical patterns.

Eucalyptus regnans 2: L 5 - 7 cm; Of 5 - 7 cm;

depth of soil A - horizon 0 - 16 cm; soil B - horizon as above.

Eucalyptus regnans 3: L 7 - 9 cm; Of 4 - 6 cm;

depth of soil A - horizon 0 - 16 cm.

4.3.4 Sample sites of exotic gymnosperm trees.
Trees of the Survey area Flagstaff.

Cryptomeria japonica: L 5 - 13 cm; Of 3 - 7 cm;

depth of soil A - horizon 0 - 17 cm.

Larix decidua: L 3 - 7 cm; Of 3 - 7 cm;

depth of soil A - horizon 0 - 15 cm.

Pinus radiata (1920): L 4 - 8 cm; Of 8 - 12 cm;

soil A - horizon pale grey; 0 - 15 cm.

Pseudotsuga menziesii: L 1 - 4 cm; Of 2 - 4 cm;

soil A - horizon dark grey; 0 - 20 cm;

soil B horizon: yellow - grey matrix 20 - 50 cm; 50 - 70 cm yellow grey, mottled yellow orange; 70 - 100 cm yellow - orange matrix with grey vertical and horizontal patterns.

Pinus radiata (1962): L 5 - 11 cm; Of 7 - 10 cm;

soil A - horizon pale grey; 0 - 15 cm;

soil B horizon: yellow - grey matrix 15 - 45 cm; 50 - 100 cm yellow grey to mottled yellow orange with grey vertical and horizontal patterns intensifying with depth.

Pinus radiata (1965): L 4 - 9 cm; Of 5 - 9 cm;

soil A - horizon pale grey; 0 - 15 cm.

Pinus radiata and *Pinus nigra*, (clearfelled in March 1993): L 0 cm, up to 150 cm (wood debris in rows); Of < 1 cm; soil A - horizon eroding, pale grey, condensed, gleyed 0 - 15 cm.

Pseudotsuga menziesii, (clearfelled in 1991): L 0 cm, 200 cm; Of <1 cm;

soil A - horizon Ah eroding, pale grey, condensed, gleyed 0 - 16 cm.

4.5   Conclusion.

The examination of the community structure and the organic layers near particular canopy trees, suggests differences in the organic matter contribution to the mineral A horizon. Under *Pinus radiata*, *Cryptomeria japonica*, *Eucalyptus regnans*, *Nothofagus spp*, and *Quercus canariensis* litter is almost exclusively from the tree canopy. Other canopy trees support an understorey of other species and this results in seasonal fluctuations in the contributions of litter to the soil from various subcanopy species (Brockie, 1992). The litter layers under the podocarps and *Plagiantus regius*, *Sophora microphylla*, *Kunzea ericioides*, the majority of exotic deciduous trees and the creek-side *Eucalyptus regnans* stand contained limited amounts of litter, contributed by indigenous subcanopy species.

This contribution, however, is unlikely to affect the comparison between individual trees significantly, for the following reasons:

> the biomass and the litter contribution of a canopy species far outweighs the contributions of subcanopy species (Walter, 1987).

> the sampling period was in summer, when indigenous trees have their maximal litter production (Brockie, 1992 p.47).

> Far fewer indigenous leaves are shed during the remainder of the year.

In addition, the position of the soil sample sites under the wide crowns of angiosperm trees minimises subcanopy contributions on an annual basis.

5 Soil Analysis Techniques.

Introduction.

The analyses of soil parameters were performed according to widely accepted, contemporary methods on samples from each of the three soil depth strata, in order to examine potential effects of any particular tree on the A - horizon.

Determinations of soil pH, soil moisture, organic matter, cation exchange capacity, the analysis of base cations (Ca^{2+}, Mg^{2+}, K^+, Na^+), total soil nitrogen and the determination of plant available phosphates followed the methods, collated by Morgan (1992). Detailed descriptions of the procedures for each method can be found in Morgan (1992); Allen, et al. (1986); Haynes (1982); New Zealand Soil Bureau, (1972); (1987); Page, et al. (1987); Smith (1975). The analysis for soil carbon and the determination of humic matter fractions were accomplished by methods that were researched and tested by the author (see 5.1; 5.2).

5.1 Methods.

The determination of field moisture content was performed immediately after collection on the samples from 7 - 8 cm. Readings of the soil pH were taken on the same day from all soil samples. Distilled water was added at the standard mixing ratio of 1 : 2.5 (soil : water). The subsequent procedure followed Morgan (1992).

The soil samples were air-dried at 20° C, sieved through a 2 mm mesh and stored in air tight containers, for further analyses. Subsamples were oven-dried at 105° C in order to obtain correction factors for variations in the soil water content of samples, which were used to adjust the results of subsequent soil analyses. Two replicates were used in each analysis and the respective accuracies were reflected in the number of significant figures (1 - 4), used to present results. Blank samples accompanied each analysis. Morgan (1992) gives the detailed description of the analytical procedures for soil organic matter content, cation exchange capacity, amounts of the cations (calcium, magnesium, potassium, sodium), amounts of total soil nitrogen and plant available phosphates. A brief description of the methods follows in the next paragraph.

5.1.2 Summary Description of Soil Analyses.

The soil moisture contents to an oven dry basis (ODM) were determined for each sample by using unsieved, air dry soil heated at 105° C for 12 hours. Calculation: Moisture% = {loss of weight on drying (g) / oven-dry weight of sample (g)} x 100.

This soil moisture factor was used to correct weight of the soil elemental analyses to oven-dry.

* Organic matter was determined by the loss on ignition after six hours at 450° C. Calculation: Organic matter content (%) = {weight loss (g) / oven-dry weight (g)} x 100.

*C.E.C. was determined by displacing various cations in the exchange complex with the ammonium ion, NH_4^+ from 1 M ammonium acetate CH_3COONH_4 The leachate contains the base cations.

The soil was re-leached with 1 M NaCl and the leachate distilled to recover the ammonium ions and to allow a measurement for concentration, by titrating the distillate with 1 M HCl-acid. The C.E.C. (in me %) can than be calculated from that information. Calculation: C.E.C. = T.E.B. (Ca^{2+}; Mg^{2+}; K^+; Na^+) + (H^+; Al^{3+}).

* Amounts of calcium and magnesium ions were determined by atomic absorption and potassium and sodium by flame emission spectra. The specific wavelengths are for Ca^{2+} (423 nanometers), for Mg^{2+} (285.2 nm), for K^+ 766.5 nm at the flame emission mode and 589 nm for sodium.

Seven standards of known concentration were used to obtain measurements of light absorption for the cations. Two samples of distilled H_2O rinsed the A.A. prior to absorption measurements on two blanks, which were followed by the samples. The calibration graphs were examined and cubic curves were fitted to obtain accurate measurements of sample cation concentrations, which were corrected by subtracting the values estimated for the blank solutions.

* The total exchangeable bases were obtained by addition of the base cations.

* The base saturation (%) was acquired by calculating: B.S. (%) = {T.E.B / C.E.C.} x 100.

* The total soil nitrogen was determined by digestion and distillation. The organic compounds in the soil sample are converted to soluble nitrate salts in solution during the digestion. The distillation procedure converts the the nitrate salts to ammonia, which is recovered and measured by titration with 0.02 M HCl.

Calculation (for a 20 ml aliquot and 0.5 g soil sample: Nitrogen (%) = total HCl ml x 0.14.

* The determination of plant available phosphates entails a procedure with two parts. The first is the extraction of available phosphates from the soil sample, using a sodium hydrogen carbonate solution (Olsen et al. 1954). The second part is the measurement of the phosphate content using an ultraviolet - visible spectrophotometer (set at 880 nm) and standards of known phosphate content. A calibration graph was prepared using the data of the ready-made standard solutions. Calculation: Olsen P (µg/g) = µg P\ml extract x 50; the figure was corrected, first by substracting the value for the blank determination and second by converting to the oven-dry weight of the soil samples.

Measurements of the exchangeable bases and the cation exchange capacity are expressed in milli-equivalents, while most other measurements are expressed as g per 100g. Measurements of plant available phosphorus are expressed in micro-grams (µg) of P per g, or as mg P per kg of oven dried soil.

For the calculation of ratios, the values of milli-equivalents were transformed into g per 100g.

according to the following formula:

for example Calcium: Ca me% x 0.5 (1 over valency) = millimoles Ca per 100 g.

Millimoles Ca /1000 = moles Ca per 100 g. Moles Ca per 100 g x 40.08 (atomic mass) = g of Ca per 100 g (%).

5.2 Modified procedures, researched and first applied for this investigation. Wet oxidation of Carbon and Humic matter fractionation.

5.2.1 Analysis of Soil Organic Carbon.

* A wet oxidation method (New Zealand Soil Bureau, 1990; Black, 1975?) was adapted and refined to determine the organic carbon contents of the soil samples. The method derived from a laboratory manual of the New Zealand Soil Bureau (1990){method 1} and from a method proposed by Kalembasa and Jenkinson (1973){method 2}. Both methods were tested independently, and a combination of both was adapted as the workable method for the soil samples. The former method

{1} describes the technique used in the Agricultural Chemistry Lab, Koronivia, Fiji for the analysis of soil and plant samples for the Fiji Soil and Crop Evaluation Project. The latter method {2} was published in "Methods of soil analysis" (Black, 1975). The refluxing of the soil - dichromate - acid solution, recommended in the latter method {2}, was found to be unnecessary (the exothermic reaction of acid mixture is sufficient) and unworkable on the soil samples, since the titration end point was not obvious with the indicator solutions, that were recommended for either of the two methods {1&2}. On the other hand it was found that the concentration of 1 N potassium dichromate, recommended in the former method {1} was higher than required for the soil samples. Controls with (0.0833 M) potassium dichromate solution, recommended in method {2} and applied at double the amount of the recommended volume of method {1}, confirmed that the same results were obtained on several consecutive soil samples, using both concentrations (1 N and 0.0833 M) at 10 ml and 20 ml respectively. The wetting of the soil samples was improved by doubling the volume. The same controls also confirmed the practicability of the 2:1 acid mixture, applied at once and left to react for 30 minutes. The saturated ferrous ammonium sulphate solution was made daily using the technique described in method {2}. The molarity (392.14) of the solution was established with two blanks, which were run prior to each set of soil samples.

The chemical reactions can be described as follows:

The soil organic matter is oxidised by dichromate ($Cr_2O_7^{2-}$) and sulphuric acid, using the heat of dilution of the sulphuric acid (120° C). Unreduced $Cr_2O_7^{2-}$ is titrated with Fe^{2+} (from ferrous ammonium sulphate) using diphenylamine as a redox indicator. Oxidation of organic matter is not complete, averaging about 77%, therefore a factor of 1.3 is applied during the calculation.

$$2\,Cr_2O_7^{2-} + 16\,H^+ + 3\,C = 4Cr^{3+} + 8\,H^+ + 3\,CO_2$$
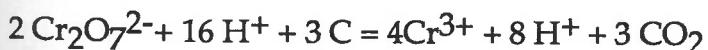
The preparation of the reagents entailed:

The dissolution of 24.52 g (0.0833 M) $K_2Cr_2O_7$ (oven dried at 105° C) in one litre of distilled water.

Concentrated sulphuric acid with a specific gravity (s.g.) of 1.84

Concentrated orthophosphoric acid, s.g. 1.75

The saturated solution of ferrous ammonium sulphate {$Fe(NH_4)_2(SO_4)_2.6H_2O$} at 0.5 M was prepared prior to each run in order to avoid crystallisation over night. 196

g of ferrous ammonium sulphate was dissolved in deionized water. 20 ml of concentrated sulphuric acid was added and the solution was topped up to 1 litre.

The indicator solution constituted of 0.5 g diphenylamine, dissolved in 100ml concentrated sulphuric acid.

The procedure commenced by weighing out 0.25 g of finely ground, air dry soil (< 0.25 mm) into a dry 500-ml conical flask.

20 ml of 0.0833 M potassium dichromate was added to the flask and gently swirled to disperse the soil and achieve complete wetting.

40 ml concentrated sulphuric acid, as well as 8 ml of phosphoric acid was added in the fume cupboard and swirled for one minute to thoroughly mix the soil with the reagents.

The solution was left for thirty minutes.

Subsequently 200 ml of water was added to the flask, and 5 drops of diphenylamine indicator.

The excess dichromate was titrated with the saturated ferrous ammonium sulphate solution. This changed the indicator colour from pale muddy blue to dark muddy blue and flashed to brilliant green at the end point, at which readings were taken.

A blank determination was carried out in the same way, without soil, to standardise the ferrous ammonium sulphate solution prior to each run of samples.

The calculations were accomplished, using the following formulas:

[A]. 10 / blank titration ml = N (normality of ferrous ammonium sulphate).

[B]. % C = (V1 -V2) x N x 0.003 x f x 100 / s

where:

V1 = ml ferrous ammonium sulphate for blank titration

V2 = ml ferrous ammonium sulphate for sample titration

N = normality of ferrous ammonium sulphate (from[A])

0.003 = weight of one milliequivalent carbon (g)

f = factor (1.3)

s = sample weight (g)

The moisture factor was used to correct to oven - dry basis.

The results of this analysis were used to compare absolute carbon values between trees and soil sections and to equate soil carbon contents with the results of the elemental analysis of the humic fractions.

5.2.2 Fractionation of Soil Humic Matter.

Introduction:

A considerable literature research on various fractionation procedures was undertaken (Kononova, 1966; Calderoni, Schnitzer, 1967, 1984; Felbeck, 1971; Smith, 1975; Chen, et al., 1978; Stevenson, 1982; Shaymukhametov et al.,1984; Swift, 1987; Parsons, 1988; Kontchou, 1989; Hammond et al. 1991; Miodragovic, 1991; a. o.) and options were discussed. The extraction method that has been recommended by the International Humic Substances Society was eventually adopted (Calderoni, Schnitzer, 1984). This method represents an eventual scientific agreement, that promises to achieve comparable results with substances, that are extremely diverse.

Technical challenges, of shaking a solution, while maintaining a pure nitrogen atmosphere were eventually solved. And after a number of trial runs the process of fractionating the soil organic material into carbonates, humic acid, fulvic acid and humines commenced. The humic acid and fulvic acid fractions were freeze-dried and a gravimetric measurement was taken. The amount of insoluble humin fractions varied considerably between different samples. Carbonates were dissolved at the first stage of fractionation and discarded.

A Carlo Erba Elemental Analyser was used to obtain measurements of carbon, nitrogen, and hydrogen contents of the humic acid and fulvic acid fractions.

5.2.2.1 The Rationale for the Choice of Methods.

The adoption of the extration procedure recommended by the International Humic Substances Society {I.H.S.S.} (Calderoni, Schnitzer, 1984; MacCarthy, et al., 1986) represents a scientifically accepted compromise to obtain comparable results with organic substances, that have posed problems for classification because of their diverse nature.

Problems of classifying the operationally defined humic isolates (fulvic acid, humic acid, and humin fractions) include that the fractionation scheme is not well in line with the biochemical processes operating during humification in soils (Oades, 1988). Several plant and microbial biopolymers (polysaccharides, lignin, peptides) have solubilities, which results in their inclusion, at least partly, in the fulvic acid or humic acid fraction.

In addition individual humic fractions are structurally diverse, which influences the rate of extraction (Kononova, 1966, Koegel-Knabner et al. 1990). These differences are caused by the plant litter quality. Mor humus type humic acids are hydrophilic and are removed completely with the first extraction, whereas humic acids that derive from the mull humus type are complexed with polyvalent cations to the mineral soil and require several extractions. It has generally been accepted that not all mull type humic acids can be extracted and that excessive mechanical stress, caused by high numbers of extractions could lead to the fracture of humic acid compounds and to a mechanically induced increase of the fulvic acid and carbonate fractions.

In consideration of the potential problems concerned with the comparison of quantitatively and qualitatively different humic compounds it was decided to subject all samples to two extractions (Koegel Knabner, 1991).

The {I.H.S.S.} procedure involves two aspects; the extraction and the purification of the humic- and fulvic acid fractions. A number of recent research papers have focussed on decoding the polymeric nature of various humic substances and the mechanisms involved in their formation (Scharpenseel, 1961; Schnitzer, 1971, et al., 1978, 1979, 1984; Swift et al., 1987; Koegel-Knabner et al. 1988, 1990, 1991, 1992; Hempfling, 1989; Kim et al., 1990; Malcolm, McCarthy, 1991; Rasyid et al., 1991). If the structure of humic substances is to be analysed by spectroscopy, the purification is an essential component of the extraction procedure.

However, the loss of some humic material during the purification process can not be prevented (Schnitzer, 1967; Stevenson, 1981) .

The primary research objective was to compare, gravimetrically the amounts of the humic fractions (Kononova et al., 1966) under various phanerophyte cover at three soil depth strata.

The loss of unpredictable amounts of humic matter during the purification process could therefore not be accepted. Gravimetric measurements were taken before and after a loss on ignition of a subsample of the freeze-dried humic matter extracts, in order to determine the amounts of the ash free and thus pure humic fractions.

A secondary research objective was concerned with possible structural differences of the humic fractions and the allocated amounts of a particular element to a humic fraction under different trees and at three soil depths.

5.2.2.2 Description of Extraction Procedure.

The extraction procedure was thus adopted with the objectives of this research and the facilities of the soil laboratory in mind.

Only distilled H_2O was used in the process. Two grams of air dried soil < 0.2 mm were weighed into a tared 50 ml screw-capped polypropylene centrifuge tube and treated as follows.

- **Step 1** Acid pretreatment: Twenty ml of 0.1 mol L^{-1} HCL were added to the soil sample, so that the equilibrium pH was between 1 and 2 and the final solution to dry soil ratio was 10 ml to 1 g. { the I.H.S.S. recommendation of 1 mol L^{-1} HCl solution was found to be far too concentrated to obtain a ratio of 10 liquid to 1 soil at pH 1 to 2.}

The test tube was capped and shaken for one hour.

- **Step 2** The supernatant, containing free carbonates and alkali earth metals, was separated form the residue by settling and centrifugation at 1700 rpm for one hour {850 rpm x g} (Calderoni, Schnitzer, 1984) and decanted.

- **Step 3** a) Five ml of H_2O^D was added to slurry the residue. The slurry was neutralized to pH 7 by adding 1 mol L^{-1} NaOH (about three ml).

b) The solution was made up to 20 ml by adding 0.1 mol L^{-1} NaOH, to attain a final extractant to residue ratio of 10 : 1. The test tubes were immediately capped and the air replaced with N_2. {This was necessary in order to prevent the possible disintegration of humic macro-molecules into smaller fragments under the combined influence of O_2 and the mechanical stresses of the following procedure}. The screw caps were specifically made and connected in three series of five to allow for the simultaneous shaking of 15 samples on two sample shakers. The screw caps allowed

the continual replacement of possible gases, emanating from the solution, with N_2 under shaking conditions, while completely preventing any mixing of sample solutions with inlaid filters.

- **Step 4** The suspension from step 3 was extracted by intermittent shaking for 12 to 16 hours under N_2. The alkaline suspension was allowed to settle overnight under N_2 and subsequently centrifuged at 1700 rpm for one hour and carefully decanted into a new tared test tube (tare weight including lid has been recorded to 1/10.000 g accuracy). The air was replaced with N_2 and the test tube closed.

The residue was subjected to a second extraction by repeating the procedure from step 3 b. Some of the 20 ml 0.1 mol L^{-1} NaOH was added and shaken manually to disperse the sediments, the lid was rinsed subsequently.

Eventually both extracts were combined in the tared test tube, adding up to 40 ml of an alkaline solution, including humic and fulvic acids. The solution was immediately subjected to step 5.

The residue of both NaOH extractions contains the insoluble humin fraction.

- **Step 5** The supernatant was acidified with 6 mol L^{-1} HCl (10 - 15 ml) under constant stirring until the pH of 1 was reached. The air was replaced with N_2 , the test tube capped and the solution was left to stand for 14 hours in cool conditions.

- **Step 6** The fractions of humic acid (solid) and fulvic acid (supernatant) were separated by centrifugation at 1700 rpm for one hour.

The supernatant, containing the fulvic acid, was carefully decanted into a new tared test tube (tare weight including lid has been recorded to 1/10,000 g accuracy). The solid humic acid and the supernatant fulvic acid were near neutralized in order to avoid possible acid damage to the freeze drier (Step 7). The humic acid was adjusted to pH 5 using a 0.1 mol NaOH solution (~5 ml). The fulvic acid supernatant was adjusted to pH 5 with 1 mol NaOH (0.4 ml - 1.3 ml). The air was replaced with N_2 in both test tubes. The test tubes were closed and stored in a freezer.

- **Step 7** The numbered and tared lids of the test tubes, containing the frozen samples were replaced with filterpaper and freeze dried.

The freeze drier was operating a vacuum at - 67^0 C, instantaneously converting H_2O from solid to gas. The vacuum was released carefully (after about 12 hours) in order to prevent any loss of matter from the freeze dried samples. The numbered lids were relaced immediately and a gravimetric measurement was taken.

- **Step 8** The samples contained the respective humic fractions and NaCl.

Light crucibles (4 - 5 grams) were tared. The salt flakes were thoroughly mixed with the humic samples and two sub-samples were placed in the tared crucibles, taking note of the exact gross and sub-sample weights. The organic amounts were determined by combustion at 700° C for 6 hours[1] (Chen et al., 1978).

Footnote:

[1] Aldrich humic acid was used as a standard with known ash content. Various temperature and time combinations were experimented with until a constant weight measurement was achieved. Sample humic acid and fulvic acid were included in the experiments. The initial temperature was 450° C, weight measurements were taken after 12, 18 and 24 hours. No organic material had combusted. Consequently the temperatures were increased by 50° C for each trial and sample weight were compared at six hourly intervals. At 600° C organic material was lost, but did not reach a constant weight after 24 hours. The weight remained constant after six hours at 700° C and ash measurements of the Aldrich humic acid reached the amounts, that were certified by the manufacturer. The fulvic acids were subjected to the same ignition time and temperature.

- **Step 9** The crucibles were allowed to cool before weighing, to determine the contents of ash. The tare weight of the crucible was subtracted from the weight of the crucible, including the ash component of the humic material. This resulted in a weight measurement of the ash, which was divided by the gross sub-sample weight prior to the combustion and multiplied by 100. This produced the ash percentage of a particular sample.

a = weight of ash residue

b = sub sample weight

Ash%= a / b x 100

- **Step 10** Calculation of humic acid % or fulvic acid %; (g per 100 grams of soil).

Humic extracts (one of two) = H. ex. (humic acid or fulvic acid fraction)

1) H. ex.% of sub-sample = 100 - ash %.

2) H. ex. in grams = H. ex. % of sub-sample x extract sample weight (Step 7).

3) H. ex. % (of soil-sample) = {H. ex. in grams / oven dry weight (from 2 g of initial soil sample weight)} x 100.

5.2.2.3   The Elemental Analysis of Humic Fractions.

Introduction

The carbon, hydrogen and nitrogen contents of the humic fractions were analysed.

All soil samples had been analysed for the total amounts of carbon and nitrogen.

The elemental composition of the humic fractions could give an indication on the structure of humic substances and on the allocations of a particular element to a specific humic fraction. Previous research (Scharpenseel, 1961, Schnitzer,1971; Koegel Knabner 1988-92) has demonstrated that humic fractions are structurally very heterogeneous with the heterogeneiety being dependent on environmental, particularly biotic factors (Malcolm & McCarthy 1991; Rasyid, 1992; chapter 7).

The absolute amounts of the humic fractions and any potential structural and elemental allocation differences in regard to the primary producers and the soil depths were of particular interest in this research.

Variations of the combined humin and carbonate fractions between trees and between soil strata were visibly very heterogeneous. An elemental analysis of the humic fractions would also provide an indication as to the nutrient content of the humin fraction and enable an estimation of the composition of the residual organic matter.

The elemental analysis had to be limited to one third of the total number of samples, due to financial constraints.

5.2.2.3.1   Methods:

Two trees each were selected at random from the indigenous, the exotic deciduous and the gymnosperm group. One tree was selected from the australian group. Both humic fractions were analysed at all three depth levels under each tree. An additional number of samples (up to one third of the total) was selected at random from various trees and soil depths and both humic fractions were analysed by the

Carlo Erba Elemental Analyser EA 1108 for contents of carbon, nitrogen and hydrogen.

The analytical method is based on the complete and instantaneous oxydation of the sample at a temperature of 1020^oC. The components (CO_2, H_2O, SO_2, N_2) are separated and detected by a thermal conductivity detector, which gives an output signal proportional to the concentration of the individual components of the mixture. The information is fed into a work station and the percentages are calculated.

The percentage measurements of the elemental contents {C; N; H} were thus obtained in duplicate from the freeze-dried samples, subsequent to (**step 7**).

Three humic fractions (H. fr.) are composed of the two humic extracts (H. ex.), humic acid and fulvic acid and of the insoluble humin fraction.

Following on from **step 10**:

- **Step 11**   In order to convert the percentage measurements to carbon (% C) or nitrogen (% N) contents of the three humic fractions (H. fr.), the following formulae were used.

1) % C in H. ex. = {% C in sub-sample (from step 7; H. ex. + NaCl)} / {% H. ex. (step 10, 1) in sub-sample (from step 7; H. ex. + NaCl)} x oven dried soil sample weight x 100.

2) % C as part of H. ex. in soil = % H. ex. (of soil-sample, step10, 3) x % C in H. ex. (step 11, 1; excluding the multiplication with oven dried weight).

Alternatively:

2) C in g of sub-sample = H. ex. + NaCl in g (from step 7) x % C in sub-sample (from step 7).

% C of H. ex. in soil = C in g of sub-sample / oven dried sample weight x 100.

3) % C in humin and carbonate (Rest - C) = % C in soil (total) - { % C as part of H. ex. (humic acid C + fulvic acid C) in soil}.

4) % of soil C as part of H. fr. = % C of H. fr.(H. ex; Rest - C) in soil (step11, 2; 3) / % C in soil (total) x 100.

The same calculations were used to acquire the results for nitrogen (N).

5.2.2.3.2 Discussion on the Elemental Analysis of Humic Fractions.

The elemental analysis of the humic fractions was accomplished by the technichians with the Carlo Erba Elemental Analyser of the Chemistry Department of the Otago University.

Dr. R. Cunninghame and Dr. B. Peak (Chemistry Deparment O.U.) expressed some concern, based on a paper by MacCarthy, (1989) with regard to sample ash contents and the possibility of interference with the accuracy of elemental measurements. The ash contents of the humic extracts were composed of mainly NaCl and minor amounts of clay impurities. The NaCl is derived from the extraction process.

An additional amount of NaCl, particularly in the fulvic acid extracts, was caused by the neutralization of the extracts prior to freeze drying.

The extract neutralization was considered to be unavoidable, in order to avoid possible damage to the freeze-dryer, which might have occurred, had the fulvic acid samples been freeze-dried at the original extraction pH of 2.

Ashing experiments with commercially available "pure" humic acid showed the amounts of ash varying around 25 %.

According to MacCarthy (1989) anomalously high oxygen values are primarily to blame for summations of elemental humic contents in excess of 100 % in samples with a high ash content.

High ash contents would therefore most probably lead to over-estimations of humic oxygen contents.

Elemental measurements of humic fraction oxygen contents were however not attempted.

While high ash contents of commercially available humic extracts seem to influence measurements of oxygen contents, it is reported to only marginally influence other elemental estimations (such as carbon, nitrogen) and at ash values of more than 60 %

(Dr. R. Morgan, Geography Dept. O.U. pers. com, 1993). At ash contents of $> 60\%$ the 5% level of confidence ($p = < 0.05$) for the elemental determinations could possibly be exceeded.

The ash contents of the sample humic fraction was generally below 60% and exceeded 60% with the fulvic fractions only, due to the necessary neutralization prior to freeze drying.

Hence, while the elemental measurements for the humic fraction can be considered accurate, the elemental measurements on the fulvic acid fractions might contain some level of inaccuracies.

A second concern of Dr. Cunningham involved the comparatively high $N : C$ ratio of the samples, when compared to commercially made humic acid. These concerns were also based on the paper by MacCarthy, 1989, which analysed the nature of commercial humic acids.

However, the C:N ratios of the samples compared very well with figures cited for various natural humic acids in Kononova's research (1966) and that of other authors (Stevenson, 1982; Koegel-Knabner et al. 1991).

Various options were discussed with Prof. Dr. A. Mark, Dr. R. Morgan and Dr. B. Peak.

There was no intention to determine the humic molecular group structure with either infrared spectroscopy or CPMAS 13C NMR spectroscopy, which would require "pure" humic extracts (Hatcher et al., 1985).

The purpose of the elemental analysis is to obtain estimates of the variation of the elements carbon and nitrogen in regard to the structural size of the humic fractions and the elemental contents that are allocated to the humic fractions and compare various quantities and ratios within a sample, as well as between soil strata and between trees.

Ash contents were individually determined and elemental measurements adjusted for the ash free extracts.

The purification would have made gravimetric measurements of the total sample contents of the extracted humic fractions impossible.

A reduction in ash is usually accompanied by significant loss of humic acid, possibly by liberation of low-molecular-weight fulvic acids bound to the humic acids through

metal linkages. A possible disadvantage is that chemical modifications may result (Stevenson, 1982).

The humic extracts originated from 2 grams of soil and some individual sample extracts, were too small to be purified.

The time and costs involved in further extract purification could not be justified and the potential for results with a margin of error slightly in excess of 5 % for elemental carbon and nitrogen was considered to be acceptable for the following reason.

Financial constraints, imposed limitations on further analyses.

1) The Carlo Erba elemental analyser was not used to obtain readings of oxygen and sulphur contents of the humic fractions.

2) Of the original number of soil samples only one third could be analysed on humic fraction elemental contents.

This limited data set was insufficient for inclusion with the other soil parameter data and a subsequent combined statistical evaluation.

However, the elemental analysis does demonstrate that there are structural differences within-, and elemental allocation differences between the humic fractions, dependent on plant litter quality and soil depth.

This analysis further indicates that an opportunity for further research exists, which will be extremely valuable for resource management decisions that are to be based on the concept of sustainablity.

As a prerequisite there is a need for a refinement of the last step of the extraction procedure. It could be attempted to omit the humic extract neutralization, prior to freeze-drying, in order to limit excess amounts of NaCl ash in the extracts. This however is only feasible if it is assured that the freeze-drying equipment will not be damaged by freeze-drying coagulated humic acid and fulvic acid in solution at a pH of 1 to 2. In addition, at these low pH values there might be problems at later stages of analyses due to the adopted extract structure in the form of rigid spherocolloids.

A multitude of options for extraction and analyses, is more than matched by the structural and the compositional diversity of the lasting organic substances, which almost eludes attempts of classification and may call for a more dynamic approach,

in order to be able to predict the direction of soil evolution following the input of a particular primary producer (Koegel-Knabner, 1988; 92).

The results of the elemental analysis of the humic fractions will be discussed in chapter seven.

6000 Parameter analyses of Soil A - horizon.

Introduction

The sections in chapter six are digitised according to the following system.

The second digit relates to various statistical treatments of the data.

The first two "second digits" describe the two ordinations, from which two sets of tree groupings originate, which were subsequently analysed and discussed comparatively.

> The P.C.A. tree groupings are discussed in section 6.1.

> The Cluster Analysis tree groupings are discussed in section 6.2

Two third digits relate to the two tree groupings under further statistical analyses.

"One" denotes the tree groups derived from the combined soil depth ordination of the P.C.A. (Section 6.x.1) and

"Two" , as third digit denotes the tree groups derived from the dendrogram of combined soil depths (Section 6.x.2)

The section 6.3 discusses the results of the analysis of variance.

The histograms of tree group means are subsequently discussed in section 6.4. Section 6.6 discusses the soil parameter correlations of tree groups at each soil depth.

Sections 6.5 and 6.7 suggest the hypotheses that follow from the results of the analyses of variance (sect. 6.5) and the correlations (sect. 6.7) respectively.

The fourth digit relates to the organizational partitioning, covering Methods, Results, Discussion.

Letters denote single soil parameters.

Figures contain the first three digits and feature a letter for a particular soil parameter.

Soil parameter results.

The results of the soil parameters are presented as table 2 in the Appendix: B.

Each tree and each soil parameter is depicted by three values representing three soil depths. For better visibility, the highest values are shown as **bold** numbers, the lowest values as *italic* numbers.

Group averages for each soil strata were gathered for the original (pre-ordinaton) tree grouping. The grouping of trees was based primarily on ecological origin (indigenous or exotic), then on classification (gymnosperms or angiosperms) and thirdly on disposition (deciduous or evergreen) in case of the angiosperm group.

The initial indications of soil nutrient variations under trees were made visible with group averages and ratios between various soil parameters.

6.1.0.0 Data Ordinations.

Introduction:

Principal Component Analysis (P.C.A.) was utilised to produce ordinations of tree species, based on the correlations of the measured pedological variables.

A number of P.C.A. ordinations were obtained to elucidate the effects of the phanerophytes on the mineral soil.

The P.C.A. derived tree groups were subjected to an analysis of variance to determine the significance of potential differences between groups for any soil parameter at any of three A-horizon depth levels. These are discussed in conjunction with the tree group means for soil parameters and soil depth strata. The soil parameter correlations of tree groups determined the significance of soil parameter relations for any of the tree groups at any one of the three soil depth levels.

A cluster analysis (sect. 6.2.0.0) established dendrograms of three soil depths, which illustrate that individual variability within a forest ecosystem might be matched by convergent tendencies between phylogenetically distant individuals of independently evolved forest ecosystems.

A dendrogram on the combined soil depths established tree groups, which were analysed and discussed in parallell with the analyses of the tree groupings derived from the P.C.A.

6.1.0.1   Principal Components Analysis: (P.C.A.):

The aim of the principal component analysis is to order the trees with respect to the underlying environmental gradients within the set of environmental data. The P.C.A. summarises the environmental data and produces an ordination of trees, based on environmental variables alone. An inspection of the graphs enabled trends in the data to be recognized, trees to be regrouped and hypotheses to be generated.

The first axis is significantly associated (eigenvectors of > 0.205 at 5 % level of significance) with increases in: pH; cation exchange capacity; total exchangeable bases; calcium; potassium; soil organic matter; carbon; nitrogen; phosphorus; humic acid and fulvic acid, and accounts for 60% of the total variation between trees.

The second axis is associated with increases in: soil organic matter; carbon; humic acid; fulvic acid and sodium. The second axis is also associated with decreases in: pH; total exchangeable bases; calcium and phosphorus. The second axis accounts for a further 11% of the total variation.

The cumulative percentage of variation accounted for by both axes is thus 71%.

A third axis (not shown) has significant component loadings for magnesium, accounting for a further 8.3 % of the total variation.

The component loadings of a fourth axis (not shown) is associated with increases in fulvic acid and phosphorus and with decreases in sodium and pH and accounts for a further 6.0 % of the total variation.

6.1.0.2 P.C.A. Results:

The first ordination used all trees and the soil parameters (pH; cation exchange capacity; base saturation; total exchangeable bases; carbon; nitrogen; phosphorus; humic acid; fulvic acid) from all three soil depth levels.

Figure 6.1 positions the trees with respect to each soil stratum on the first two axes of the P.C.A.

Figures 6.1.a - c show the positions of the trees at each soil section.
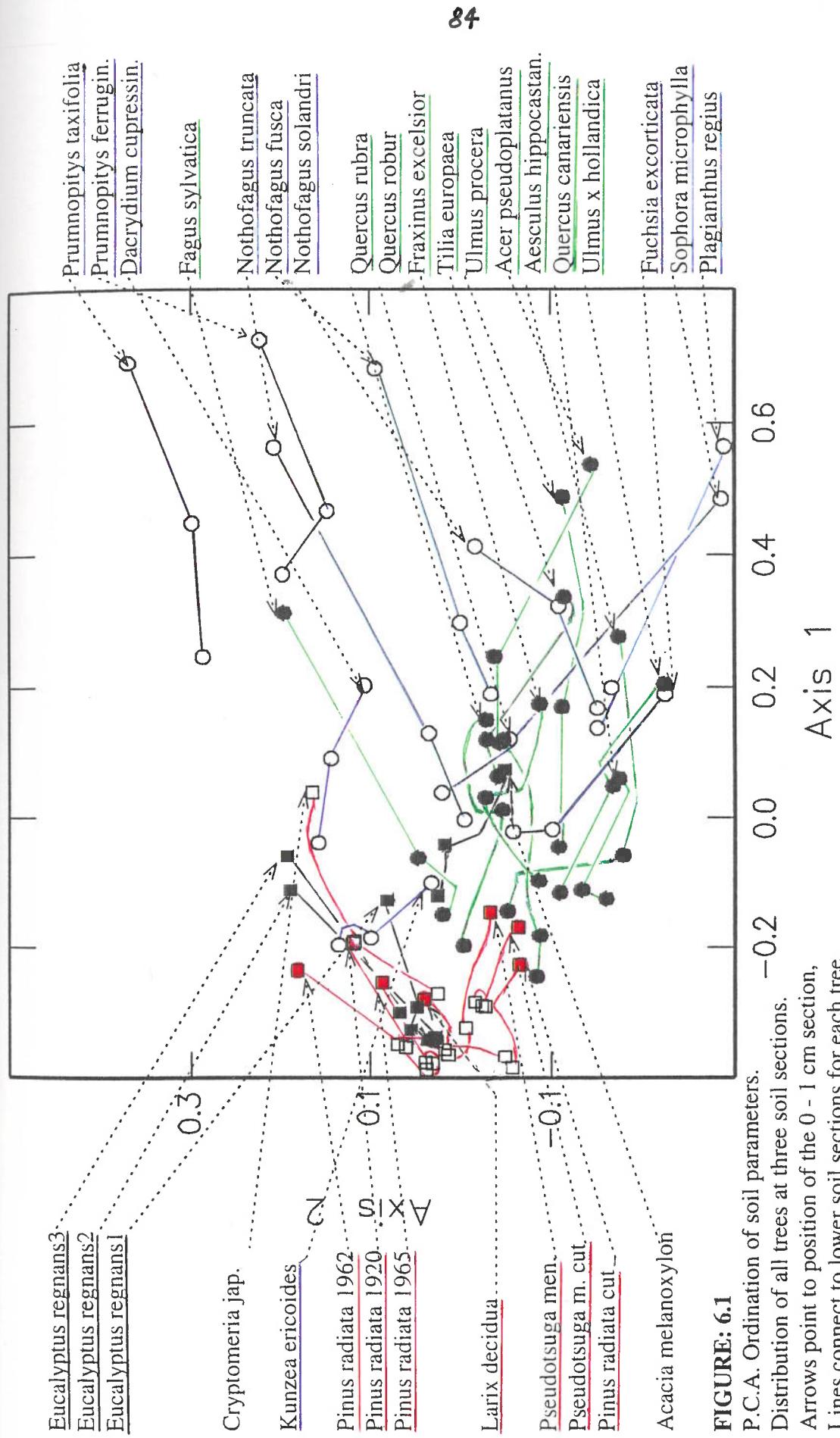
FIGURE: 6.1

P.C.A. Ordination of soil parameters.
Distribution of all trees at three soil sections.
Arrows point to position of the 0 - 1 cm section,
Lines connect to lower soil sections for each tree.

FIGURE: 6.1.a
P.C.A. of soil parameters
Distribution of trees at 0 - 1 cm.

Indigenous trees:

Exotic trees;
Deciduous trees:

Pyrophanerophyte
group:

Eucalyptus regnans:

Pinaceae:
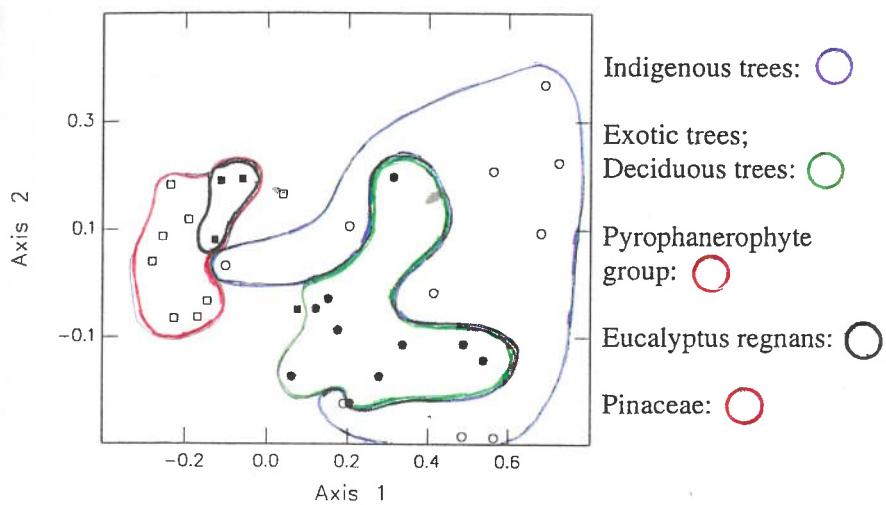
FIGURE: 6.1.b
P.C.A. of soil parameters
Distribution of trees at 7 - 8 cm.

Indigenous trees:

Exotic trees;
Deciduous trees:

Pyrophanerophyte
group:

Eucalyptus regnans:

Pinaceae:
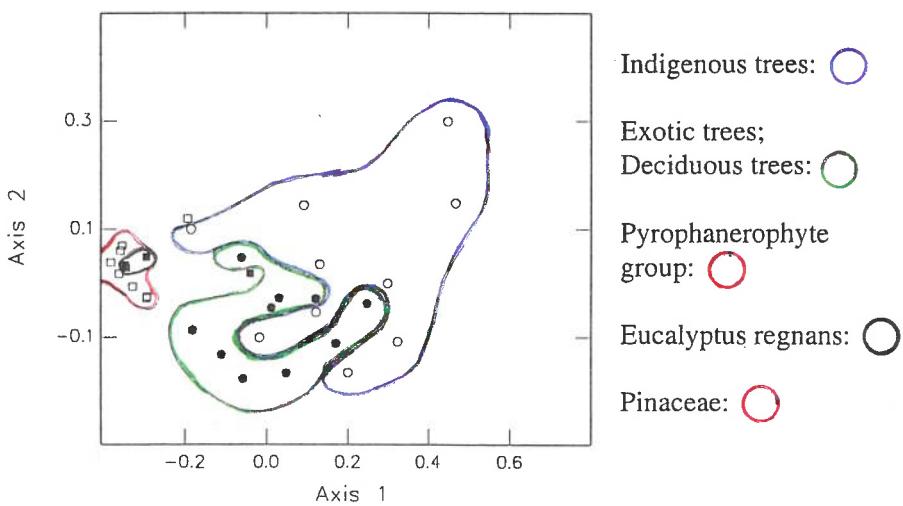
FIGURE: 6.1.c
P.C.A. of soil parameters
Distribution of trees at 14 - 15 cm.

Indigenous trees:

Exotic trees;
Deciduous trees:

Pyrophanerophyte
group:

Eucalyptus regnans:

Pinaceae:
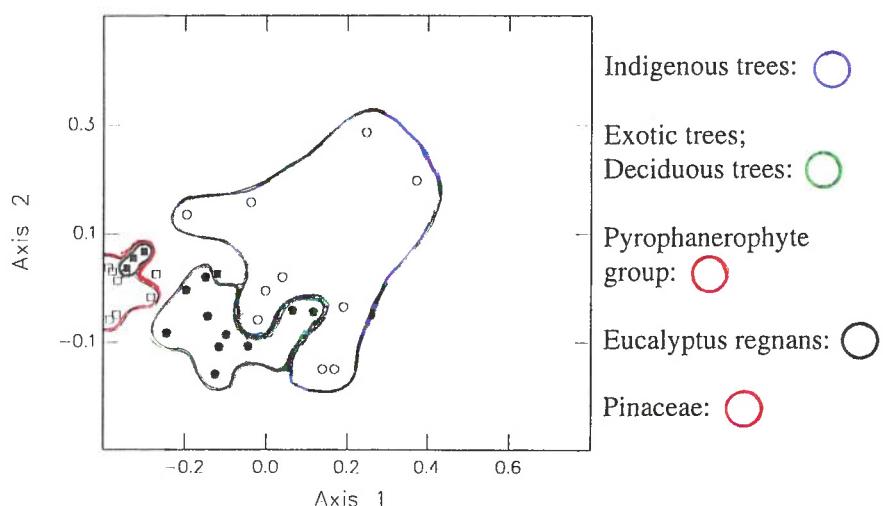
If the three soil depths for each tree are connected (Fig. 6.1), a trend of individual tree influence on the mineral soil becomes obvious, radiating, with decreasing soil depth, from a common homogeneous mineral soil, which would be situated at the centre left of the ordination.

The *Pinaceae* and *Eucalyptus regnans* display a very restricted differentiation between the soil depth levels. Any influences at the upper soil levels are directed towards the top right of the ordination, which is associated with increases in soil organic matter and decreases of pH, exchangeable bases and phosphorus.

Pseudotsuga menziesii and the two clearfelled sites also display restricted influences, but the position of their uppermost soil level towards the lower right of the ordination indicates an association with soil organic matter breakdown and nutrient release.

Most other trees display significant individual influences on the soil.

The indigenous canopy and emergent trees of the genera *Nothofagus* and *Prumnopitys* and to some extent *Dacrydium*, as well as the exotic deciduous canopy species *Fagus sylvatica* and to some extent *Cryptomeria japonica*, display trends towards the upper right of the ordination, which are in general (first axis) associated with increases of soil organic matter, cation exchange sites on humic fractions and the major soil nutrients (Ca, K, N, P), whereas their position on the second axis reinforces their association with increases of soil organic matter, the humic fractions, carbon and sodium but also indicates lesser increases of exchangeable bases, pH, calcium and phosphorus than shown by trees towards the bottom right of the ordination. These trends are most pronounced at the upper soil depth level.

The majority of the sampled trees, including the <u>indigenous deciduous trees</u> *Fuchsia excorticata*, *Plagianthus regius*, and *Sophora microphylla; Kunzea ericoides* and all other <u>exotic deciduous angiosperm trees</u> trend towards the lower right of the ordination, which is associated with increases in soil organic matter, including the humic fractions, and increases of exchangeable bases, nitrogen, phosphorus and pH.

The genera *Acer, Aesculus, Fraxinus, Fuchsia, Plagianthus, Sophora, Tilia* and *Ulmus*, show a greater influence on soil characteristics than *Acacia, Quercus* and especially *Kunzea*.

Subsequent ordinations (Figs. 6.1 a - c) show positions of trees with respect to soil depths.

The <u>indigenous</u> and <u>exotic deciduous angiosperms</u> are widely dispersed and intermingled on the ordinations. (Figs. 6.1, depths a - c)

The *Pinaceae* and the eucalypts remain a distinct cluster.

The dispersion for all trees decreases with soil depth.

The ordination depicts a general trend of decreased differentiation between trees with soil depth.

This supports the notion that trees alter the soil characteristics rather than soil characteristics determine the occurrence of the trees.

The Australian *Acacia melanoxylon* seems to have a similar influence on the soil to *Quercus robur*, based on the trend over the three soil depths and the position with respect to the upper-most soil stratum at (0 - 1 cm). *Acacia melanoxylon's* positions at the two lower soil strata (7 - 8 cm and 14 - 15 cm) is very similar to these of *Fagus sylvatica*.

The myrtaceous *Kunzea ericoides* exhibits another individual trend. It is the only indigenous tree placed close to the distinct and tightly clustered group of exotic trees from the *Pinaceae* and *Myrtaceae* (australian eucalypts). *Kunzea* however, tends towards the lower right of the P.C.A., showing a similar trend with depth to other indigenous subcanopy trees and the emergent *Dacrydium cupressinum*. The separation between the soil depths for *Kunzea ericoides* is, however, slight, indicating little differentiation in the soil A-horizon.

6.1.0.3 Discussion on Principal Component Analysis results.

The tight clustering of the exotic *Pinaceae* and *Myrtaceae* is indicative of a common ecological strategy, distinctly different from all other trees.

For further analyses both genera were grouped together as **pyrophanerophytes (firetrees)**.

The name of this group derived from a common adaptation of the tree species (phanerophyte*) to recurring events of disturbance.

A pyrophyte is a plant, adapted to withstand or to achieve a competitive advantage from fire (Allaby, 1994).

* A phanerophyte is one of Raunkiaer's (1922) life form categories, being a plant whose perennating buds or shoot apices are borne on aerial shoots.

Eucalyptus regnans has been classified as being a pyrophyte, adapted to long intervals between intense fires, which are fuelled by large litter loads. (Pryor, 1976).

There is under *Cryptomeria japonica* (Taxodiaceae) more differentiation between the soil strata, than under the *Pinaceae*. However, increases of soil organic matter are also associated with decreases of total exchangeable bases, pH and phosphorus. The influence of *Cryptomeria japonica* on the upper-most soil stratum is similar to that exhibited by *Eucalyptus regnans* or *Dacrydium cupressinum*.

At the mid-soil stratum (7 - 8 cm) , both *Cryptomeria japonica* and *Kunzea ericoides* are associated with higher levels of soil organic matter and humic fractions than the quite distinctly clustered group of *Pinaceae* and the exotic *Myrtaceae*. At the lowest soil stratum of 14 - 15 cm, *Cryptomeria japonica* is situated half-way between the deciduous angiosperm group and the tightly clustered group of *Pinaceae* and exotic *Myrtaceae*. The nearest genera within the deciduous group are *Quercus* and *Fagus*.

Thomson and Simpson (1935) recorded high pH values under *Melicytus ramiflorus*, *Griselinia littoralis*, and *Myoporum laetum*. High to medium pH values were recorded in soils under *Dacrycarpus dacrydioides*, *Podocarpus totara*, *Podocarpus halii* and *Prumnopitys taxifolia*. Acidic conditions were recorded by the same authors under *Dacrydium cupressinum* and *Nothofagus menziesii*. The conclusion was reached by Thomson and Simpson that: "each species definitely influences the reaction of the soil in its immediate vicinity."

6.1.0.4 Grouping of trees, based on the P.C.A. Ordination.

The P.C.A. ordinations allow a regrouping of trees, based on the correlations between soil parameters. Accordingly the trees were grouped by:

> 1) significant differences in their effects upon upper soil horizons, indicating different nutrient cycling habits and

> 2) ecological origin

Ecological origin was maintained as a means of sub-dividing the broad group of indigenous and exotic deciduous species, embodying diverse, nutrient cycling trends, which have broadly similar effects upon the soil, but with strategies that seem to be species and niche specific.

One very distinct cluster of trees emerged from this initial ordination of soil parameters. This is the group of **pyrophanerophytes**, including the genera *Pinus*, *Pseudotsuga, Larix* and *Eucalyptus*.

All other trees do not display distinct differences and any division, based on the spread of species on the P.C.A. ordination, would be arbitrary. Therefore the original grouping, based on origin was maintained, namely the **indigenous trees** and the **exotic deciduous angiosperm** trees.

Cryptomeria japonica and *Acacia melanoxylon* do not fit well with any of these three groups (see Appendix: A; 2.4 - 2.5). *Acacia melanoxylon* affects soil in a similar way to *Quercus robur* and *Fagus sylvatica*, yet is not deciduous.

Acacia melanoxylon has an ecological distribution, which covers two distinct forest ecosystems with large differences in canopy species composition. *Acacia melanoxylon* attains optimal growth as a canopy species in the Australian cool temperate rainforest in association with *Nothofagus* and gymnosperm species, but also grows as a subcanopy species within pyrophytic *Eucalyptus* forests on moister sites (Pryor, 1976; Boland, 1985) (for details, consult Appendix: A; 2.5).

Consequently, it would be inconsistent to group *Acacia melanoxylon* on the basis of origin with the genus *Eucalyptus* in the group of pyrophanerophytes.

Cryptomeria japonica also demonstrates divergent nutrient cycling strategies on the P.C.A. ordination. Once widespread, the Taxodiaceae, much like the Podocarpaceae, have a rather restricted distribution around the humid, oceanically influenced parts of the continents (Parker 1982; Raven 1986) (for details, consult Appendix: A; 2.4).

On these ecological grounds *Crypotomeria japonica* can not justifiably be grouped with the pyrophanerophytes.

Consequently, both *Acacia* and *Cryptomeria* were not included in further analyses, based on the tree groupings that derived from the P.C.A. ordination.

Kunzea ericoides' P.C.A. placement between the pyrophanerophyte group and the indigenous trees made its assignment to a tree group dependent on other considerations. While the small differentiation between soil depths is a feature common to most exotic pyrophanerophytes, it is also a feature of *Dacrydium cupressinum*. However, *Kunzea ericoides* differs distinctly from the exotic pyrophanerophytes in its trend from the upper left towards the lower right of the P.C.A. with decreasing soil depth, showing a similar trend with depth to other

indigenous subcanopy trees and the emergent *Dacrydium cupressinum*. For these reasons *Kunzea ericoides* was grouped with the other indigenous trees.

6.1.0.5 Hypotheses:

The research hypothesis endeavours to find an answer to the following question.

RH: Is there a measurable influence of trees, at the soil chemistry level, on an initially homogeneous soil substrate?

The research hypothesis gave rise to the null hypothesis:

H_o 1:"The influence on the soil of all examined trees is the same."

The Ordination of tree species, based on the analysis of principal components in the form of measured soil parameters at three soil depths, clearly indicates that **individual trees direct the genesis of the soil in a variety of ways.**

A trend of decreased separation of the position of trees on the ordination, with increasing soil depth, supports the notion that **trees do modify soil characteristics.**

Consequently, the **null hypothesis**, stating that

"all trees have similar effects on the soil"

can tentatively be rejected and the following alternative hypotheses accepted, subject to confirmation by analyses of variance:

> 1)   Individual tree species have individual influences on soil develpoment.
>
> 2)   Pyrophanerophytes display distinctly different strategies with regard to nutrient acquisition and turn-over, when compared to indigenous and exotic deciduous angiosperms.
>
> 3) Trees of distant phylogenetic and ecological origin can have convergent nutrient cycling strategies
>
> for example: (*Pinaceae* and *Myrtaceae*; certain indigenous and deciduous canopy spp., possibly *Nothofagus* and *Fagus*; *Cryptomeria* and *Dacrydium*; certain indigenous sub-canopy spp. and exotic deciduous angiosperm trees).

A second null hypothesis will be tested with the analysis of variance:

H.$_O$ 2: There is no difference between the tree groupings in the soil parameters, the amounts of the humic fractions and their particular ratios.

Further detailed analyses will include analyses of variance of soil parameters between the three tree groups. These will be conducted to confirm H$_A$ 1, H$_A$ 2 and H$_A$ 3 and to possibly obtain results for new hypotheses.

Significant correlations between soil parameters will test further hypotheses, concerned with tree group strategies.

6.1.0.6 General impressions

The tight clustering of the <u>pyrophanerophytes</u> demonstrates similar strategies for trees that commonly grow in forests with little tree species diversity, adapted to sites that are marginal for forest growth. The harsh edaphic and climatic conditions of natural pyrophanerophytic ecosystems caused the evolution of features that specialise in nutrient extraction (Walter, 1987; Delcourt, 1987; Pryor, 1976).

The wide distribution of the <u>indigenous trees</u> on the ordination demonstrates a variety of individual contributions to a coherent forest ecosystem.

Some emergent gymnosperms and the *Nothofagus* canopy trees seem to efficiently relocate nutrient cations before abscission. This results in a litter load, with carbon compounds that resist decomposition.

Tight internal nutrient cycling also explains the ability of *Dacrydium cupressinum* to grow on leached, nutrient deficient substrates in regions of high precipitation and areas with high watertables. This feature is shared by many tropical trees that grow on nutrient poor terra rossa substrates (Reichholf, 1990). In such systems the transferral of nutrients between individuals and species might mainly occur through mycorrhizal networks (Harley, 1987).

Other indigenous canopy and subcanopy species display nutrient cycles, which favour the association of a soil fauna that creates a mull humus type. The nutrients, which are cycled with throughfall and litter are balanced and encourage microbial growth and organic-mineral complexation, which minimizes ecosystem nutrient loss.

Both nutrient cycling strategies are an adaptation to New Zealands temperate maritime climate.

The <u>exotic deciduous angiosperms</u> naturally share a climatically similar (less oceanic) region, in the northern hemisphere, as spatial neighbours or in temporal succession and display similar individual nutrient cycling strategies (Walter, 1987, Delcourt, 1987). *Fagus sylvatica* and the *Cryptomeria japonica* display trends similar to *Nothofagus* and *Dacrydium*. *Ulmus, Fraxinus, Tilia* display similar nutrient cycling strategies as the indigenous genera *Plagianthus, Sophora* and *Fuchsia*.

The Appendix: A, contains a detailed description and reference list on relevant strategies and forest ecosystem dynamics.

6.2.0.0   Cluster Analysis (C.A.).

Introduction.

The ordination derived from the principal component analysis demonstrated

> that trees have individual effects on soil development;

> that indigenous and exotic deciduous trees tend to increase the soil nutrient storage capacity;

> and that the tree group of pyrophanerophytes has a distinctly degenerative influence on the soil quality, which is based on nutrient acquisition.

The results of these ordinations showed a distinct grouping of trees, between temperate climate trees that have evolved very differently in many aspects. However, the indigenous and exotic deciduous trees exhibited much variation and little differentiation. A division other than the one based on origin would have been arbitrary.

The cluster analysis provides the possibility of dividing the indigenous and exotic deciduous trees into mixed groups, entirely based on their relationships to soil parameters.

This numerical method of classification is defined as objective in the sense of repeatability (Kent, Coker 1992).

In addition, a numerical classification in form of a cluster analysis of trees based on soil parameters should show distinct levels of similarity or dissimilarity that should facilitate an ecological interpretation of the data and show any similarities between phylogenetically distant individuals.

Subtle convergent strategies are indicated between various members of the indigenous forests and the exotic deciduous forests.

It could be postulated, for example, that canopy species or sub-canopy species from both, the northern and southern Hemisphere temperate forest biomes evolved similar nutrient cycling strategies. *Nothofagus* and *Fagus*, or *Cryptomeria* and *Dacrydium* seem likely candidates showing convergent effects on the soil.

These subtleties will be explored with the cluster analysis of trees, based on soil parameters.

The tree grouping, derived from the combined soil depth levels will be subjected to an analysis of variance and to correlations of soil parameters.

6.2.0.1 Methods.

The cluster analysis uses an unweighted pair group method operating an algorithm derived from the generalized clustering procedure of Lance & Williams (1966). The Canberra coefficient is used and is based on the following arithmetics;

$$\sum (x-y \ / \ x+y),$$

where x is the score for a variable for one tree and y for the other tree under comparison. The Canberra coefficient is a distance measure that allows similarities to be calculated from different variables. In this case the coefficient (k) for the maximum value of dissimilarity on the Y-axes is set at 13, representing 13 soil variables. The dendrogram of trees, representing the combined soil depth levels has 39 as the maximum value of dissimilarity.

However, as many of the variables do not include zero values, the actual maximum difference is less than the theoretical. Crude estimates of the differences can be made by dividing the values of similarity by 13 (39) and expressing the values as percentage. Hence, a value of 6.5 denotes a similarity of 50 % and a coefficient value of 3.25 equals 75 % similarity (25% dissimilarity) for all soil parameters between individual species.

Analyses were made for the three separate soil depths, as well as for the combined soil depths.

6.2.0.2 Results.

6.2.0.3 Dendrogram based on the combined soil strata:

This dendrogram has two major branches, each of which contains at least two sub-divisions, which again branch into more sub-groups containing two to six individuals.

The variable associations of indigenous and deciduous trees, as described in the analyses for each soil depth are condensed into distinct groups.

The quotation marks denote that the groups are not entirely composed of trees that would naturally belong to any of the particular groups.

Three groups can be defined from this dendrogram. An "indigenous" group, a "deciduous" group and a "pyrophanerophyte" group. The "pyrophanerophyte" group is more or less constant throughout. The only members that show affinity to other groups at particular depth levels are *Kunzea ericoides* and *Cryptomeria japonica*. This group remains stable at 96%.

The core of pyrophanerophytes is divided at 72% similarity, into one sub-group containing the *Pinaceae* at similarities ranging from 75 - 85% and another sub-group comprising all *Eucalyptus regnans* with similarities ranging from 86% to 89%. *Eucalyptus regnans* is adjoined by *Kunzea ericoides* at 77% similarity. Both belong to the *Myrtaceae*. *Cryptomeria japonica* is associated with *Kunzea ericoides* at a similarity of 80%.

The pyrophanerophyte group significantly differs from the other main group, composed of indigenous trees and exotic deciduous angiosperms at a level of dissimilarity of 44%.

The indigenous and exotic deciduous angiosperms are divided into several sub-groups.

The "indigenous"group is relatively constant throughout the depth levels (84 %). The *Prumnopitys spp.,* *Nothofagus fusca* and *N. truncata* are constant members, which form a distinct indigenous subgroup at the top soil level. The only member, which show shifts of allegiance are *Sophora microphylla* at the lowest soil level. This group is joined by *Fuchsia excorticata,* and *Aesculus hippocastanum* at the top soil level, *Dacrydium cupressinum* at the mid soil level, and *Fraxinus excelsior* at the lowest soil depth level.

The deciduous group is perhaps the least constant over the soil depths at 79%. Its constant members are *Fagus sylvatica, Quercus spp., Acacia melanoxylon, Ulmus x hollandica.*

The numbers of indigenous and exotic deciduous trees in each of two main sub-groups, divided at 72% similarity, produce a ratio of 7 : 3 and 2 : 7 respectively. The latter sub-group contains also *Acacia melanoxylon.*

Hence, one sub-group is predominantly indigenous, while the other is predominantly composed of exotic trees.

However, the closest core relationships within the predominantly indigenous group are:

1) *Acer pseudoplatanus* and *Nothofagus fusca* (87% similarity), which are joined by *Nothofagus solandri* at a similarity of 84%.

2) *Ulmus procera* and *Tilia europaea* (86% similarity), which are associated with the deciduous *Plagianthus regius* at a similarity of 85%.

Nothofagus truncata and *Sophora microphylla* (83% similarity) are joined to this "indigenous" core at 80% similarity and *Prumnopitys taxifolia* and *Prumnopitys ferruginea* abut at a similarity level of 76%.

The predominantly deciduous sub-group has formed around two pairs, namely *Aesculus hippocastaneum* and *Ulmus x hollandica,* (88% similarity) and *Quercus robur* and *Acacia melanoxylon* (87% similarity). The latter pair is joined by *Fagus sylvatica* at a similarity of 85% and the trio by *Dacrydium cupressinum* at 83%. This association differs to some extent (80% similarity) from the group joined to the first pair.

Aesculus hippocastanum and *Ulmus x hollandica* are joined by *Fraxinus excelsior* at a similarity of 84% and the trio by *Fuchsia excorticata* at 83%. *Quercus canariensis* and *Quercus robur* (87% similarity) join this group as a satellite pair, with a similarity level of 81%.

Dendrogram based on the combined soil sections

Figure: 6.2.1

Dacrydium cup.
Fagus syl.
Quercus. rob.
Acacia mel.
Fuchsia exc.
Aesculus hip.
Ulmus hol.
Fraxinus exc.
Quercus can.
Quercus rub.
Prumnopitys fer.
Prumnopitys tax.
Nothofagus fus.
Acer pse.
Nothofagus sol.
Plagianthus reg.
Tilia eur.
Ulmus pro.
Nothofagus tru.
Sophora mic.
Kunzea eri.
Cryptomeria jap.
Eucalyptus reg. 1
Eucalyptus reg. 2
Eucalyptus reg. 3
Larix dec.
Pseudotsuga men.
Pseudots. men. cut
Pinus rad. cut
Pinus rad. 1920
Pinus rad. 1962
Pinus rad. 1965

17.22   12.92   8.61   4.31   0

6.2.0.4 Description of the dendrogram, derived from the

0 - 1 cm soil depth:

The distinct group of pyrophanerophytes (dissimilarity of 39%) consists of two sub-groups (25% dissimilarity). One contains *Pinus radiata* and *Larix decidua*,(at similarities of 89% to 78%) the other contains *Pseudotsuga menziesii*, *Kunzea ericoides* (88% similarity) and the clear-felled sites, which can be distinguished (with 20%) from the three *Eucalyptus regnans* samples at 90% similarity.

All other indigenous trees and exotic deciduous trees and *Cryptomeria japonica* form a separate group, with a soil parameter dissimilarity of 39%.

An indigenous core group of canopy-forming *Nothofagus* species and emergent *Prumnopitys* species distinguishes itself (30%dissimilarity) from all other exotic deciduous and indigenous trees.

One sub-group relates species of *Quercus* with *Acacia melanoxylon*, *Fraxinus excelsior* and *Ulmus x hollandica* at similarities of 92-86%.

Fagus sylvatica is somewhat distinct at 81% similarity, but associated with *Cryptomeria japonica* and *Dacrydium cupressinum* (88% similarity).

The other sub-group consists of four exotic deciduous trees and four indigenous trees, two of which are deciduous, namely *Plagianthus regius* and *Fuchsia excorticata*. The latter one bridges over to the previously discussed subgroup.

Acer pseudoplatanus and *Nothofagus solandri* show similar effects on the soil at this level (87% similarity). *Plagianthus regius* and *Sophora microphylla* are similarly positioned at 86% similarity and next to a close group of *Aesculus hippocastaneum*, *Tilia europaea* and *Ulmus procera*, with a similarity of 91-88%.

Dendrogram of upper soil section (0-1 cm)

Figure: 6.2.2

Dacrydium cup.
Cryptomeria jap.
Fagus syl.
Fraxinus exc.
Quercus rob.
Acacia mel.
Ulmus hol.
Quercus can.
Quercus rub.
Fuchsia exc.
Nothofagus sol.
Acer pse.
Plagianthus reg.
Sophora mic.
Aesculus hip.
Tilia eur.
Ulmus pro.
Prumnopitys fer.
Nothofagus fus.
Prumnopitys tax.
Nothofagus tru.
Kunzea eri.
Pseudotsuga men.
Pseudots. men. cut
Pinus rad. cut
Eucalyptus reg. 1
Eucalyptus reg. 3
Eucalyptus reg. 2
Larix dec.
Pinus rad. 1962
Pinus rad. 1965
Pinus rad. 1920

6.2.0.5 Description of the dendrogram, derived from the

7 - 8 cm soil depth:

The pyrophanerophyte group with the permanent genera *Pinus*, *Pseudotsuga*, *Larix* and *Eucalyptus* is again distinctly different with a dissimilarity of 47%, to all deciduous angiosperms and most indigenous trees. At this soil depth *Kunzea ericoides* and *Cryptomeria japonica* are associated with each other at 80 % similarity and, at some distance (30% dissimilarity), to the core group of pyrophanerophytes.

The indigenous and exotic deciduous angiosperm group is fairly homogeneous and branches into two main sub-groups, distinguished by 27% dissimilarity.

The indigenous canopy-tree core-assemblage of the upper soil horizon is less distinct to the other trees and comprises the emergent podocarps *Prumnopitys taxifolia* and *P. ferruginea* and at some distance *Dacrydium cupressinum* at similarities of 78-80%. The *Nothofagus* canopy trees are closely associated with *Acer pseudoplatanus*, *Ulmus procera*, *Tilia europaea*, *Sophora microphylla* and *Plagianthus regius*, at similarities ranging from 83-92%. The three exotic deciduous angiosperms, *Sophora microphylla*, as well as *Nothofagus fusca* and *N. truncata* constitute the core of this sub-group.

The core of the second sub-group consists of three pairs, *Aesculus hippocastanum* and *Ulmus x hollandica* (88% similarity), *Quercus robur* and *Acacia melanoxylon* (86% similarity) and *Fraxinus excelsior* and *Fuchsia excorticata* (82% similarity). The pair, *Quercus canariensis* and *Quercus* robur (88% similarity) join this core at 79% similarity and *Fagus sylvatica* attaches to the combined sub-group at 78% similarity.

Dendrogram of mid-soil section (7-8 cm)

Figure: 6.2.3

Dacrydium cup.
Nothofagus fus.
Acer pse.
Ulmus pro.
Nothofagus tru.
Sophora mic.
Tilia eur.
Plagianthus reg.
Nothofagus sol.
Prumnopitys fer.
Prumnopitys tax.
Fuchsia exc.
Fraxinus exc.
Aesculus hip.
Ulmus hol.
Quercus rob.
Acacia mel.
Quercus can.
Quercus rub.
Fagus syl.
Kunzea eri.
Cryptomeria jap.
Larix dec.
Pinus rad. 1962
Pinus rad. 1965
Pinus rad. 1920
Pseudotsuga men.
Pseudots. men. cut
Pinus rad. cut
Eucalyptus reg. 1
Eucalyptus reg. 2
Eucalyptus reg. 3

6.2.0.5 Description of the dendrogram,

derived from 14 - 15 cm soil depth:

The two main branches of this dendrogram again differentiate between the pyrophanerophytes and the group of indigenous and exotic deciduous trees.

The level of dissimilarity between the groups is 48 %.

At this soil depth, *Cryptomeria japonica* is associated with a clear-felled site and part of the pyrophanerophyte branch at similarities of 75-68%.

Kunzea ericoides however, is now associated with the indigenous and deciduous group.

The main group of indigenous and exotic deciduous trees divides into two sub-groups at a similarity measure of 72%.

The mainly indigenous sub-group is congregated around three pairs, each being composed of one exotic deciduous species and one indigenous species. These are *Nothofagus truncata* and *Fraxinus excelsior* (87% similarity), *Nothofagus fusca* and *Acer pseudoplatanus* (88% similarity) and *Fuchsia excorticata* and *Ulmus procera* (85% similarity). *Tilia europaea* is associated with the first pair (85% similarity) and the third pair is associated with the three preceeding species. The associates of *Nothofagus fusca* and *Acer pseudoplatanus* are allied with *Plagianthus regius* and with *Nothofagus solandri* (84 - 86% similarity).

The permanent core of *Prumnopitys taxifolia* and *P. ferruginea* (87% similarity) joins this sub-group at a similarity of 77%.

The second sub-group is based around the associates of *Quercus robur* and *Fagus sylvatica* (90% similarity) and *Quercus canariensis* and *Ulmus x hollandica* (90% similarity). The former deciduous pair is closely associated with *Acacia melanoxylon* at 85% similarity. *Dacrydium cupressinum* joins this trio at 80% similarity. *Kunzea ericoides* adjoins these with a similarity of 78%.

The other core group of *Quercus canariensis* and *Ulmus x hollandica* is associated with *Aesculus hippocastaneum*. *Quercus robur* joins this trio, which is joined by *Sophora microphylla* at levels of similarity ranging from 90 - 79%.

Both cores and their associates combine at a level of similarity of 75% to form the predominantly exotic deciduous sub-group.

Dendrogram of lower soil section (14-15 cm)   Figure: 6.2.4

Dacrydium cup.
Fagus syl.
Quercus rob.
Acacia mel.
Kunzea eri.
Sophora mic.
Aesculus hip.
Quercus can.
Ulmus hol.
Quercus rub.
Prumnopitys fer.
Prumnopitys tax.
Fuchsia exc.
Ulmus pro.
Nothofagus tru.
Fraxinus exc.
Tilia eur.
Nothofagus fus.
Acer pse.
Plagianthus reg.
Nothofagus sol.
Cryptomeria jap.
Pseudots. men. cut
Pinus rad. 1920
Pinus rad. 1962
Pinus rad. 1965
Larix dec.
Pseudotsuga men.
Eucalyptus reg. 1
Eucalyptus reg. 2
Eucalyptus reg. 3
Pinus rad. cut

6.3.0.0   ANOVA between Tree-groups of P.C.A. and C.A. ordinations.

Introduction.

Descriptive statistics were obtained for each soil stratum and each tree group, as defined by the combined depths P.C.A. ordination and the cluster analysis (C.A.). Some data were logarithmically transformed to produce a more normal distribution of values for analyses of variance.

Analyses of variance were used for each soil parameter and each soil depth strata to determine, whether differences between tree groups were significant. The results are described first for the P.C.A. tree groupings (sect. 6.3.1), {Figs. 6.3.1. a-q} then for the tree groups based on the combined soil depth dendrogram (sect. 6.3.2), {Figs. 6.3.2. a-q}.

6.3.0.1   Methods.

Where appropriate, data were log - transformed to ensure a more normal distribution of values around their mean. Where zero values occurred, the smallest value in the data set was added to all values in the set before transformation.

Hypotheses to be tested: two tailed; for each soil parameter, at each soil depth strata, between tree classification groups.

Single factor ANOVA: single factor = treegroup; variable = soil parameters; level of factors are the soil strata.

H_O = no difference between tree groups.

H_A = significant differences between tree groups.

Significant differences are displayed as arrows between tree groups for each soil parameter and at individual soil depth levels (Figures 6.3.1. a-q; 6.3.2. a-q).

A two-factor ANOVA compared the variance of C.A. tree groups over the three soil depth levels.

The combined soil strata graphics (Figs. 6.3.2. a-q), are derived from the two factor analysis of variance.

The soil parameter data of the depth strata within the tree groups was inspected on the normality of distribution. The critical values for g1 at a confidence level of $p < 0.05$ for a one tailed test were 0.645 (two tailed 0.785) for the combined count of 32 replicates for each soil parameter and at each soil strata. Counts of replicates of some elemental measurements on humic matter were lower and the critical values of g1 for skewness were adjusted accordingly.

Where the distribution was positively skewed and in excess of the critical values of g1 the entire set of soil parameter data was logarithmically transformed. A logarithm in base 10 was utilized. In three soil parameter columns the smallest value was added (K ; Na and fulvic acid carbon) to avoid logarithms of zero and possible distortions of the data. The formula utilized was $X' = \log_{10}(X+Y)$. The transformed data thus enabled parametric testing, using a one way analysis of variance and a correlation of soil parameters.

The mean was seldom less than the median and never in excess of the critical values of g1. Hence no exponential data transformation was required. Platykurtic or leptokurtic distributions of values were observed at some soil parameters. However data transformation was not attempted in order to minimize any distortions on the true measurements.

6.3.1.2   P.C.A. ANOVA Results.

The analysis of variance confirms the significance of the differences observed and described in conjunction with the P.C.A. ordination, the dendrograms and the charts.

For the <u>P.C.A based tree grouping,</u>

> the differences between the pyrophanerophytes (fire trees) and
>
> both, the indigenous trees and the exotic deciduous trees
>
> are significant
>
> at all three soil depth levels for the following soil parameters:

pH; cation exchange capacity; total exchangeable bases; base saturation; carbon; nitrogen; phosphorus and humic acid.

At the same time there are

> no significant differences
>
> between the indigenous trees and the exotic deciduous angiosperms
>
> at all soil depth levels for the following parameters:

pH; cation exchange capacity; total exchangeable bases; base saturation and nitrogen.

Furthermore there are no differences between the indigenous trees and the exotic deciduous trees at the upper soil level for the amounts of **phosphorus** and **fulvic acid** at both upper and mid soil level.

The **fulvic acid** differences between exotic deciduous trees and the fire trees were not significant at the upper and the lowest soil level.

The differences were significant

between all tree associations and at all soil depth levels for **carbon** and **humic acid** and **for phosphorus** at both of the lower soil levels.

FIGURE 6.3.1

ANOVA graphic, showing significant differences at ($p < 0.05$) between tree groupings, for each soil section and -parameter.
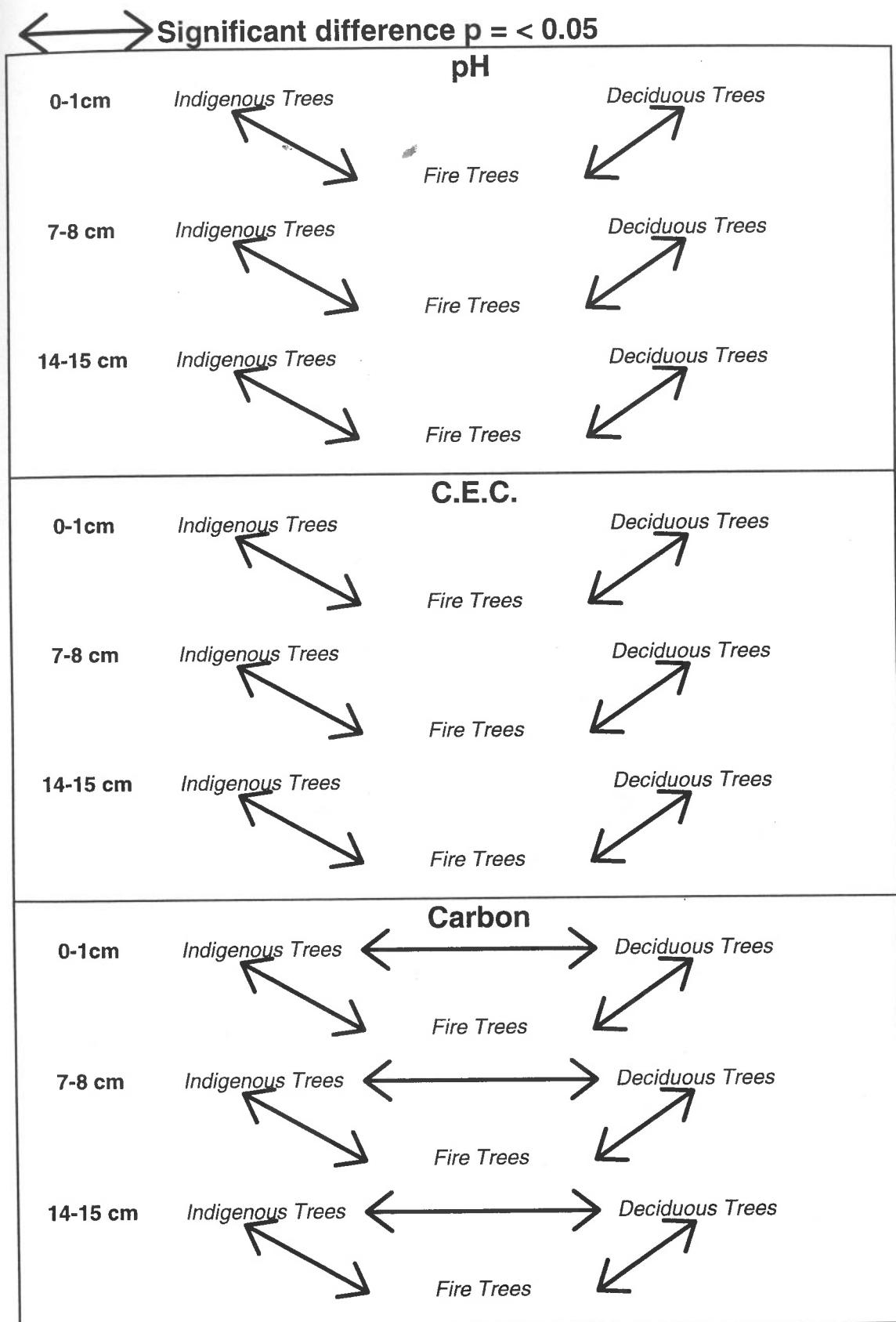
FIGURE: 6.3.1

Single factor ANOVA
P.C.A. tree groups,
Arrows denote differences at
p = < 0.05.

FIGURE: 6.3.1

Single factor ANOVA
P.C.A. tree groups,
Arrows denote differences at
p = < 0.05.
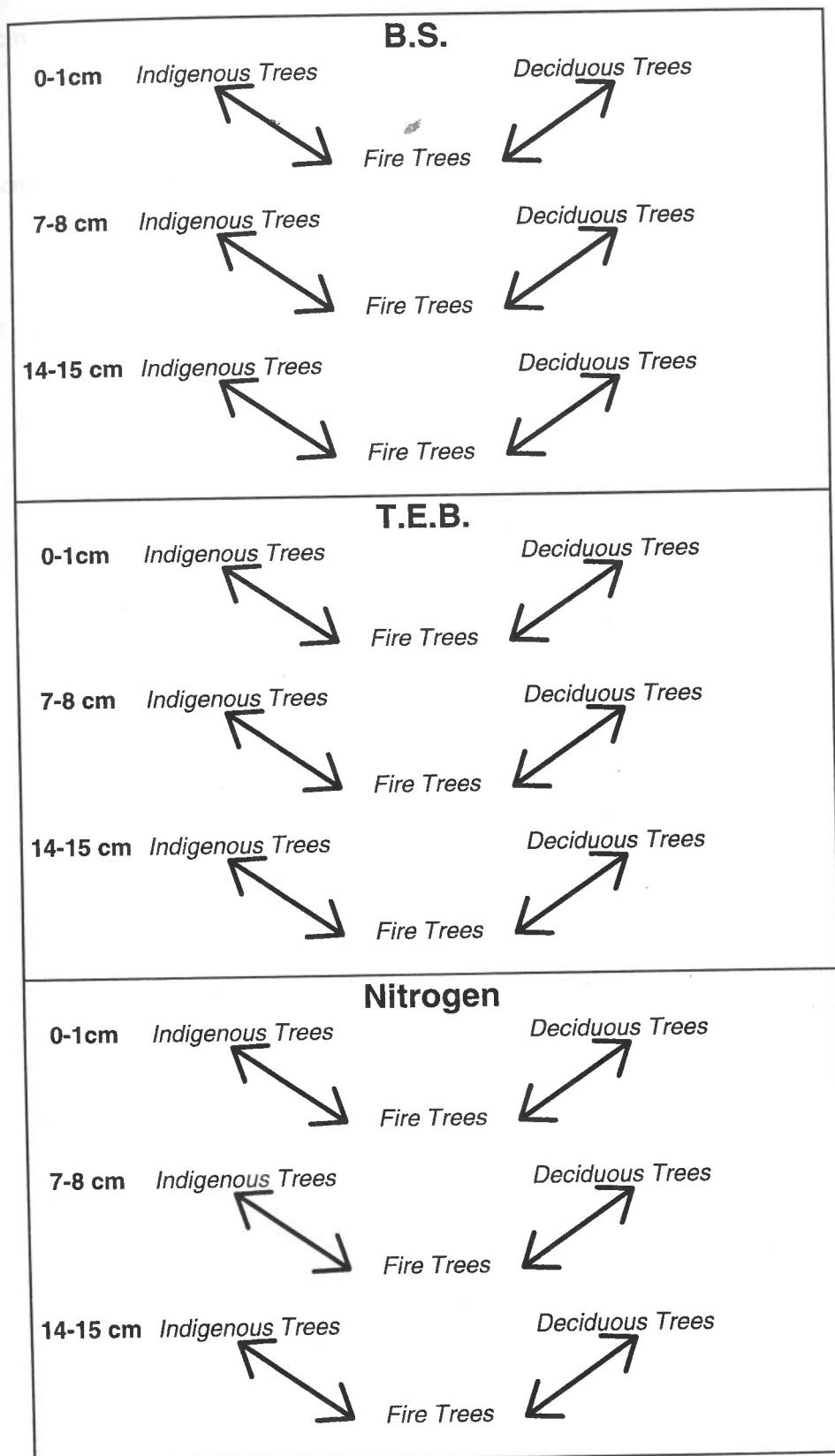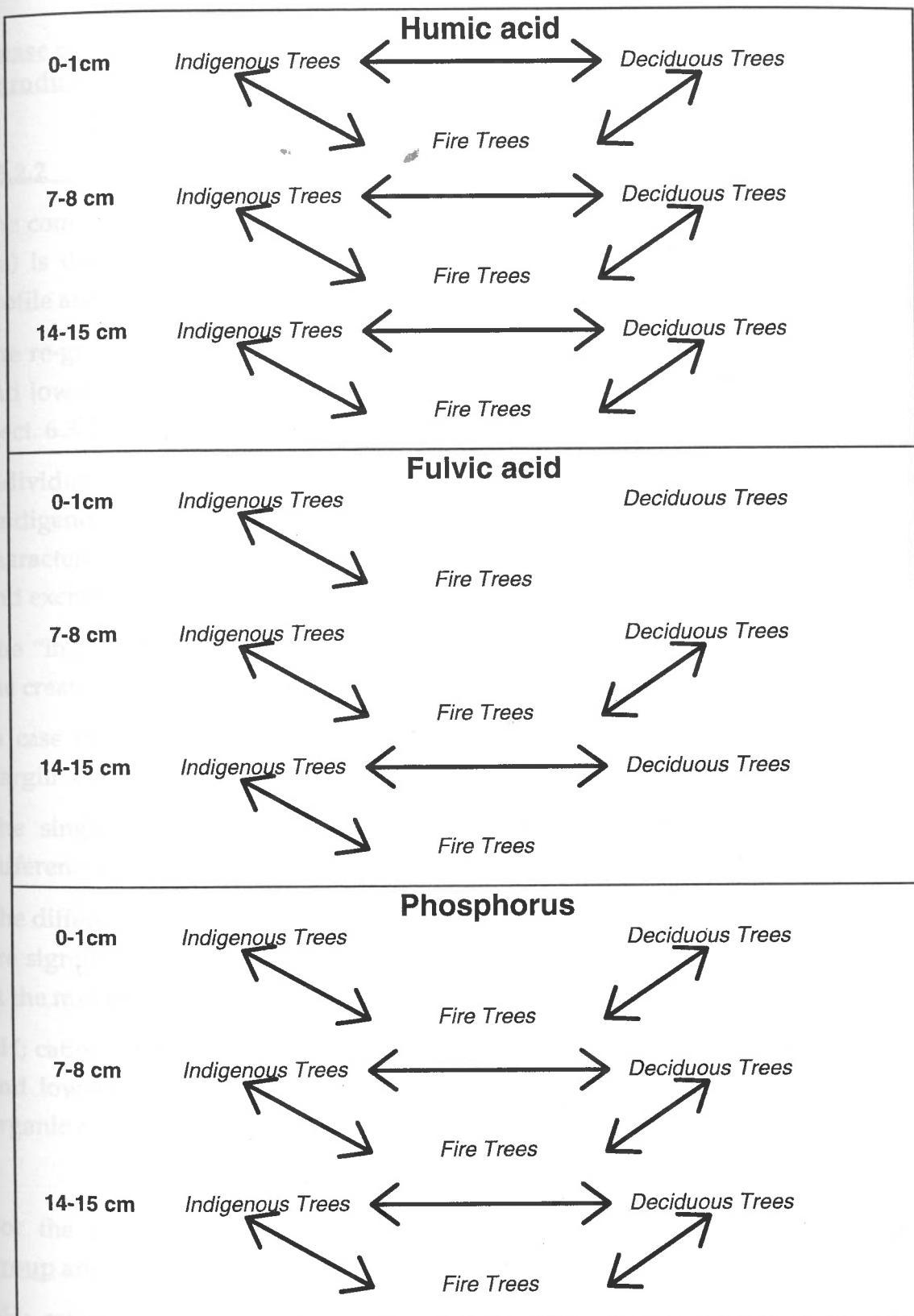
FIGURE: 6.3.1

6.3.2.2   Analysis of Variance of Dendrogram Tree-groups.

Please refer to sections 6.3.0.0 and 6.3.0.1 for Introduction and Methods on the ANOVA.

6.3.2.2   Results.

The common denominator for all soil parameter measurements (except for Mg and Na) is that the "indigenous" group shows the highest means throughout the soil profile and the *Pinaceae* demonstrate the lowest means.

The re-grouping of deciduous trees and indigenous trees led to accentuated means and lower standard errors, compared with the tree groups of the P.C.A. ordination (Sect. 6.3.1).

Individual values for soil parameters (Appendix: B; Table 2) illustrate that the "indigenous" group comprises indigenous and deciduous trees that are characterized by high amounts of both, carbon and associated parameters (C.E.C), and exchangeable bases.

The "indigenous" group therefore consists largely of trees that are very efficient in the creation of nutrient storage capacity.

In case of the two *Prumnopitys spp.* a site specific influence (the undisturbed Mt. Cargill site) on some high soil parameter values must again be taken into account.

The single factor analysis of variance largely confirms the significance of the differences, described with respect to the tree groups from the P.C.A. ordination.

The differences between the "pyrophanerophyte" group and the "indigenous" group are significant at all three soil depth levels for almost all soil parameters (except Mg at the mid soil level) and most ratios:

pH; cation exchange capacity; total exchangeable bases; calcium; magnesium (upper and lowest soil level); potassium; sodium; base saturation; nitrogen; phosphorus; organic matter; soil moisture; carbon; humic acid; fulvic acid and humin.

For the following soil parameters, the differences between "pyrophanerophyte" group and the "deciduous" group are significant at all three soil depth levels:

pH; cation exchange capacity; total exchangeable bases; calcium; potassium; base saturation; nitrogen; phosphorus; soil moisture; humic acid.

The differences are significant between "pyrophanerophyte" group and the "deciduous" group for the following soil parameters and for all soil depth levels except for the upper soil level: magnesium; organic matter; carbon; humin.

Significant differences exist between the "indigenous" group and the "deciduous" group for the following soil parameters and

... at all soil depth levels: base saturation; total exchangeable bases; calcium; potassium; sodium; cation exchange capacity; organic matter; humic acid; carbon.

...only at the upper soil level: magnesium; fulvic acid.

...only at the mid soil level: field to air dry soil moisture; magnesium; nitrogen.

The Pinaceae and the myrtax group show significant differences for the following soil parameters and

...at all soil depth levels: magnesium; organic matter; humin.

...at the upper soil level: sodium; fulvic acid; nitrogen.

...at the mid and/or lower soil depth level: field to air dry soil moisture; base saturation; total exchangeable bases; potassium; sodium; humic acid; carbon.

The graphics show significant differences between the "indigenous" group or the "deciduous" group and the Pinaceae or the myrtax group.

Generally the differences are significant at all soil depths for all soil parameters between the "indigenous" group and the Pinaceae, as well as between the "deciduous" group and the Pinaceae.

Most soil parameters are significantly different between both, the "indigenous" and the "deciduous" groups, and the myrtax group.

As shown in the histograms, the myrtax group has higher means than the Pinaceae and therefore the differences, especially to the "deciduous" group are not significant for a minority of soil parameters and soil depth levels.

Two Factor ANOVA

The graphics, depicting the combined soil strata are derived from a **two factor analysis of variance**. The groups are significantly different from each other with

respect to most soil parameters, except that the "indigenous" and "deciduous" groups show no significant differences for the following parameters: phosphorus.

The differences between "pyrophanerophyte" group and "indigenous" group are significant for all soil parameters, except Mg.

The differences between "pyrophanerophyte" group and "deciduous" group are significant for all soil parameters, except for Na.

The two factor analysis shows no significant differences between the Pinaceae and the myrtax group for following soil parameters:

phosphorus; fulvic acid; nitrogen.

Significant differences at a confidence level of 95% (p = < 0.05) are indicated by arrows.

The two factor anova compares the "Indigenous" group, the "Deciduous" group and the "Pyrophanerophyte" group with each other and at the three soil depths. It seperately compares the Pinaceae sub-group with the Myrtaceae; Taxodiaceae sub-group.
The single factor anova allows direct comparisons between all groups at each soil strata for each soil parameter.
The group means are included in brackets.
Abbreviations: grp. = group; Tax. = Taxodiaceae

ANOVA,
Dendrogram tree groups,
Arrows denote differences at p = < 0.05.

FIGURE: 6.3.2

ANOVA,
Dendrogram tree groups,
Arrows denote differences at p = < 0.05.

FIGURE: 6.3.2

115

ANOVA,
Dendrogram tree groups,
Arrows denote differences at p = < 0.05.

FIGURE: 6.3.2

ANOVA,
Dendrogram tree groups,
Arrows denote differences at p = < 0.05.
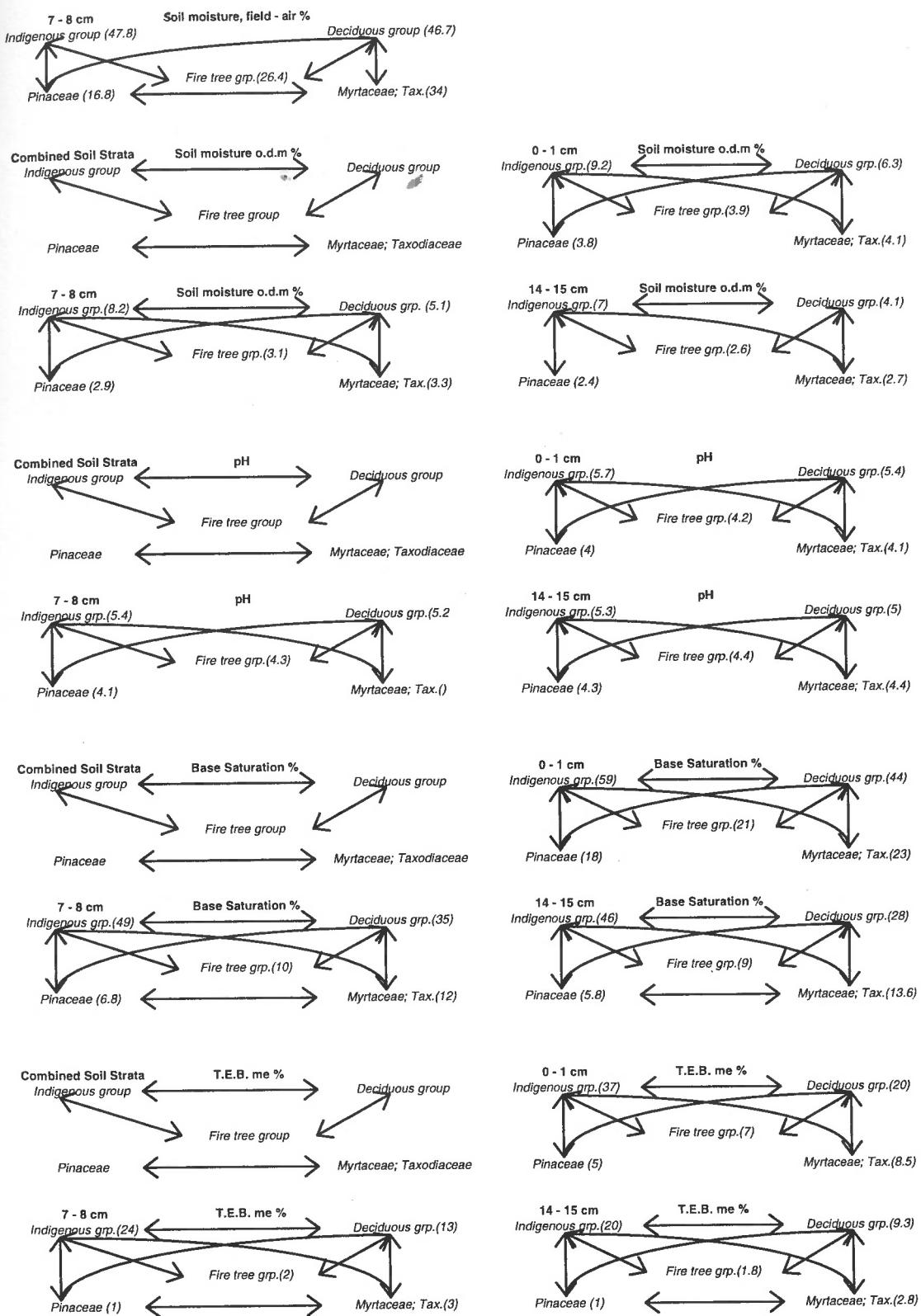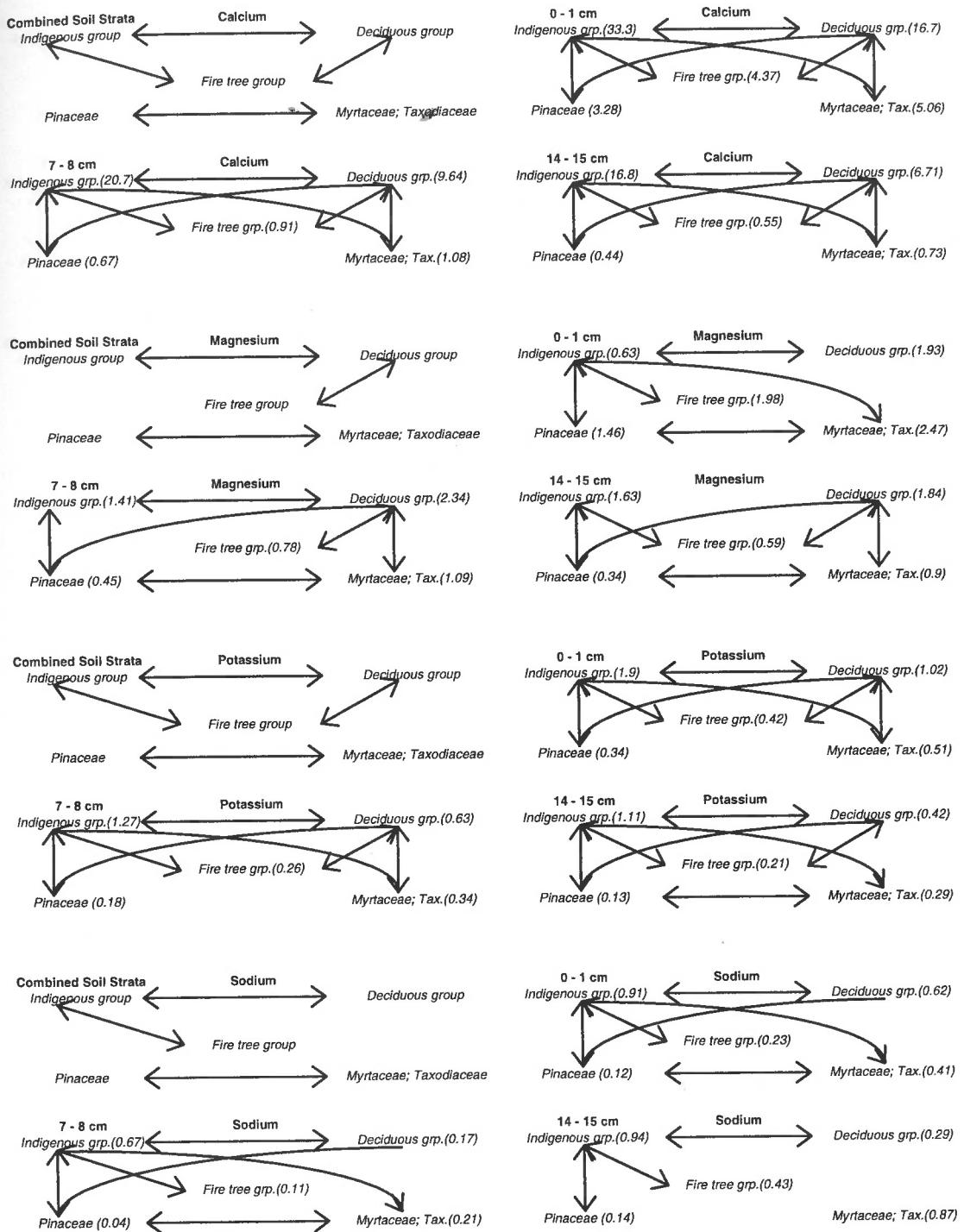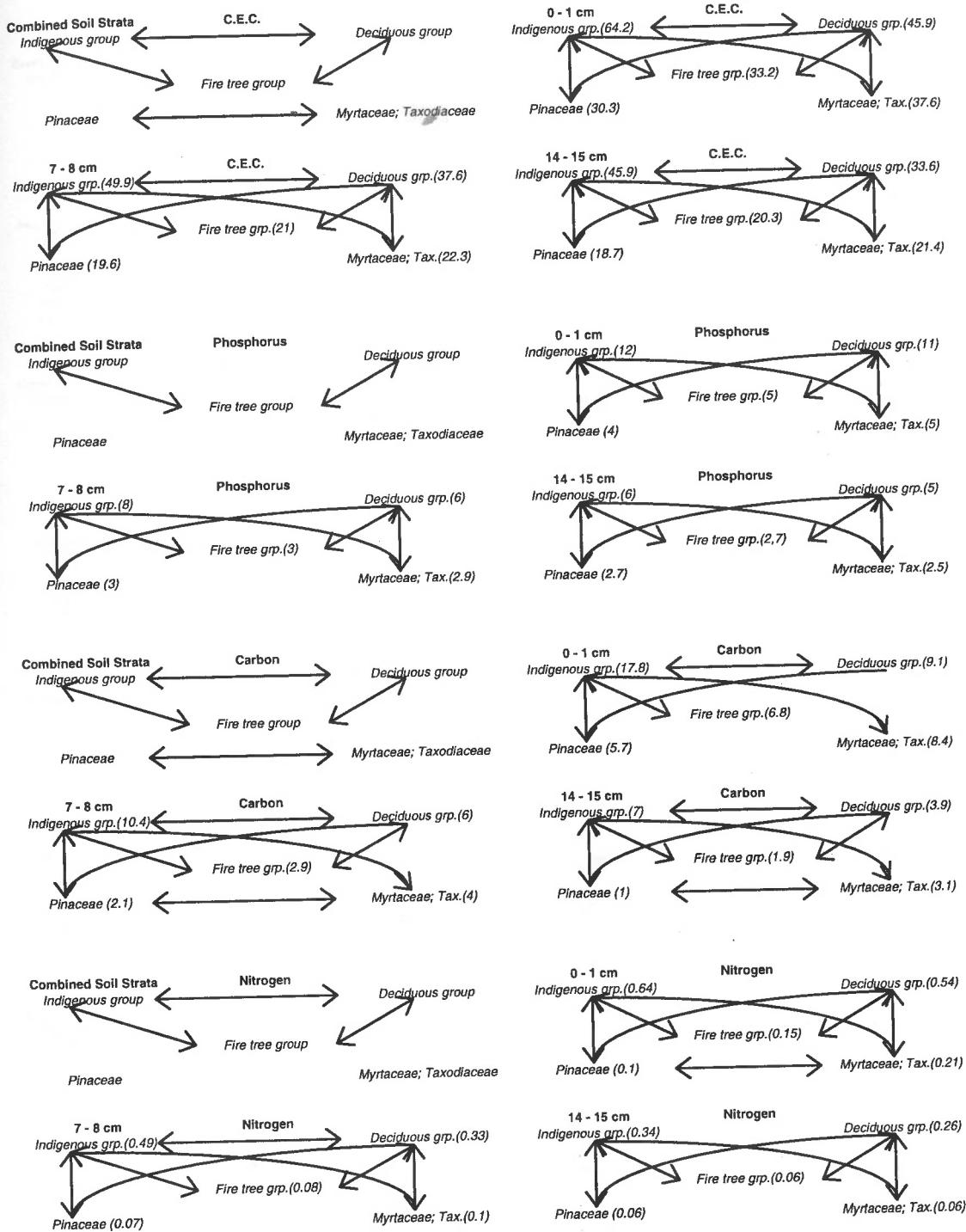
FIGURE: 6.3.2
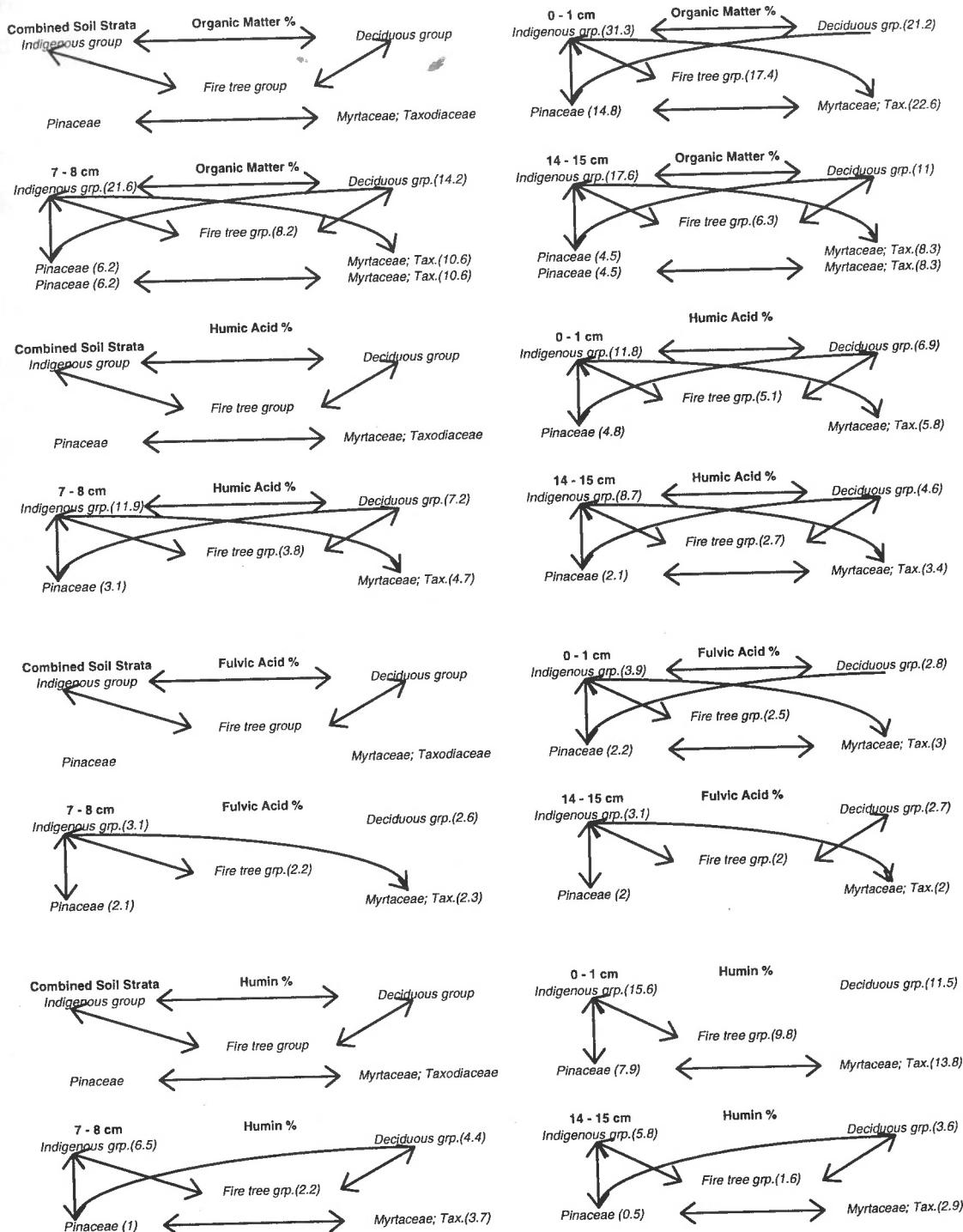
<u>6.4.0.0</u>   <u>Soil Parameter Means</u>

<u>Introduction</u>

Figures (6.4.1 a-q) display data on the means and the standard error of the **P.C.A** based **tree groups**, at the three soil depth levels.

Figures (6.4.2. a-q) display data on the means and the standard error of **dendrogram tree groups**, at the three soil depth levels.

A set of three columns represents three soil depths of a particular tree group.

Research by Tomlinson and Leslie, (1977) provided values of the soil series mineral contribution for certain soil parameters. Where available, these were added to the top left of figures (6.4.1 a-q) for reference. The mineral contribution to the pH values were measured by the author.

Wherever appropriate, the description of the histograms will refer to the tables of soil parameter results in Appendix: B; Table 2.

The charts (Fig. 6.4.2 a-q) display data on the means and the standard errors of all trees in the "indigenous" group, the "deciduous" group and the "pyrophanerophyte" group, at the three soil depth levels.

The "pyrophanerophyte" group comprises members of three families. The *Pinaceae* form a distinct group. The *Myrtaceae* and the single member of the *Taxodiaceae* combine to form another distinct group. The combined group of *Myrtaceae* and *Taxodiaceae* will be referred to as the **myrtax group** in the text of the following sections of this chapter. Soil parameter histograms for the pyrophanerophyte sub-groups "Pinaceae and myrtax" are included in Figures 6.4.2. a-q.

<u>6.4.0.2 Means Results</u>

<u>6.4.1.2.a: pH (Fig. 6.4.1.a.):</u>

The measurements of soil pH give a first indication of different tendencies in the cycling of nutrients. A pH level of 4.9 was typical for the mineral soil of the

Dunedin, Opoho and Warepa soil series and represents a baseline parameter for unmodified parent material.

Highest means were measured under the exotic deciduous trees at all soil depth levels.

While the pH under indigenous trees and exotic deciduous angiosperm trees increases from the lower to the upper soil-strata this trend is reversed under the family of *Pinatae* and the species *Eucalyptus regnans* (Appendix: B; Table 2).

Soil-pH tends to decrease under firetrees towards the uppermost soil level.

The soil A-horizon pH under pyrophanerophytes is well below that of the mineral substrate pH.

The distinct trends in soil pH are indicative of a predominance of nutrient extraction- over nutrient cycling strategies amongst pyrophanerophytes.

The combination of litter leachate, root and mycelial exudations of firetrees and associated ectomycorrhizae increases the hydrogen ion load in the mineral soil horizon (Marschner, Romheld, 1983; Marschner, 1986; Leyval, 1990). Lowered pH values are associated with increases of mineral wheathering (Jenny, 1980; Schröder, 1983; Stevenson, 1986). The weathered nutrient ions are incorporated into the biomass of the pyrophanerophyte. Initial mineral soil reserves and the buffer capacity determine the speed of soil degeneration towards a toxic and irrecoverable Al^{3+} buffer range (Ulrich, 1987).

6.4.2.2.a: pH (Fig. 6.4.2.a.):

The **pH levels of dendrogram groups** again show opposite trends between "pyrophanerophyte"group and the "indigenous" and "deciduous" groups. The pH level increases on average under both, "indigenous" group and "deciduous" group towards the uppermost soil level, whereas decreasing pH levels are noted under the "pyrophanerophyte" group and its constituents the myrtax group and the *Pinaceae*. Highest means were measured under the "indigenous" group at all soil depth levels and the lowest means under the *Pinaceae*.

FIGURE: 6.4.1.a

pH

■ 0 - 1 cm ▨ 7 - 8 cm □ 14 - 15 cm

FIGURE: 6.4.2.a

pH

□ 0 - 1 cm ▨ 7 - 8 cm □ 14 - 15 cm
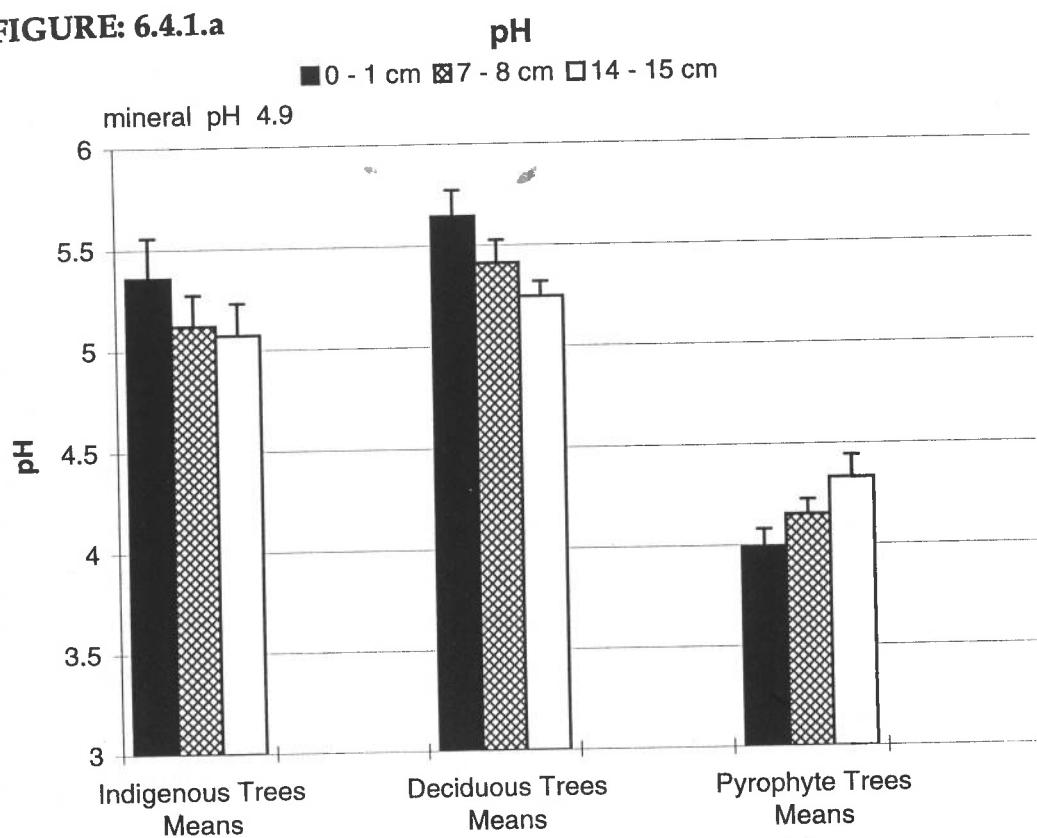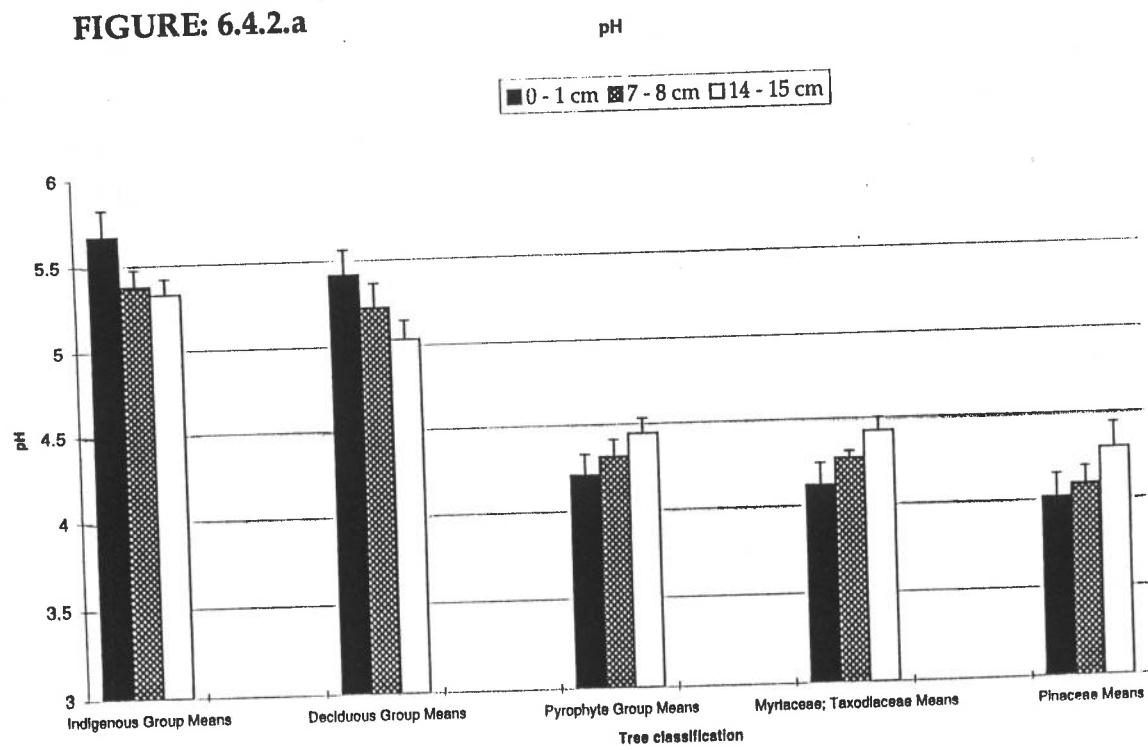
6.4.1.2.b: Soil moisture (Fig. 6.4.1.ba; bb).

The loss of moisture (m.) from field moisture to air dry condition (measured at the mid soil strata) and further moisture loss from air dry to oven dry (o.d.m.) gives some indication as to the interception capabilities of the vegetation and particularly to the water holding capacity of the soil, differences of which should be able to be correlated to the amount and structure of the soil organic material.

The soil moisture loss from field to air dry condition is very similar under the indigenous and deciduous groups. The pyrophanerophytes, however have comparably very little water stored in the soil. The groups display a stepped reduction of soil moisture loss from air to oven dry conditions, decreasing with soil depth, and from the indigenous group to the deciduous -, and the fire tree group.

The moisture contents (m. and o.d.m.) of the soil under the eucalypts and the exotic gymnosperms (Appendix: B; Table 2), in particular the standing *Pinatae* is substantially less than measurements of the soil moisture contents under the indigenous and the exotic deciduous trees.

A decrease of soil moisture loss can be correlated to an increase in soil bulk density (Schroeder, 1983).

Soil moisture of dendrogram grouping (Fig. 6.4.2b) retention capacities are correlated with soil contents of organic matter. The graph demonstrates significant differences in soil moisture between the groups. The soil moisture means of the "indigenous" and "deciduous" groups are significantly higher at all soil depth levels, as well as on drying from air to field and from field to oven dry conditions, when compared to the "pyrophanerophyte" group. The *Pinaceae* display the lowest soil moisture contents.

FIGURE: 6.4.1.b

Soil Moisture; field to air dry
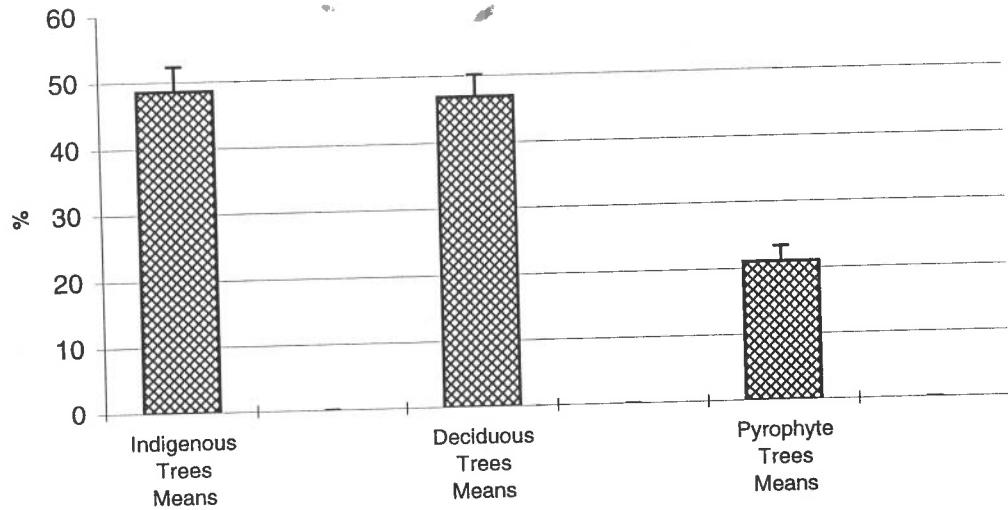
Soil Moisture; air to oven dry

FIGURE: 6.4.2.b

Soil Moisture
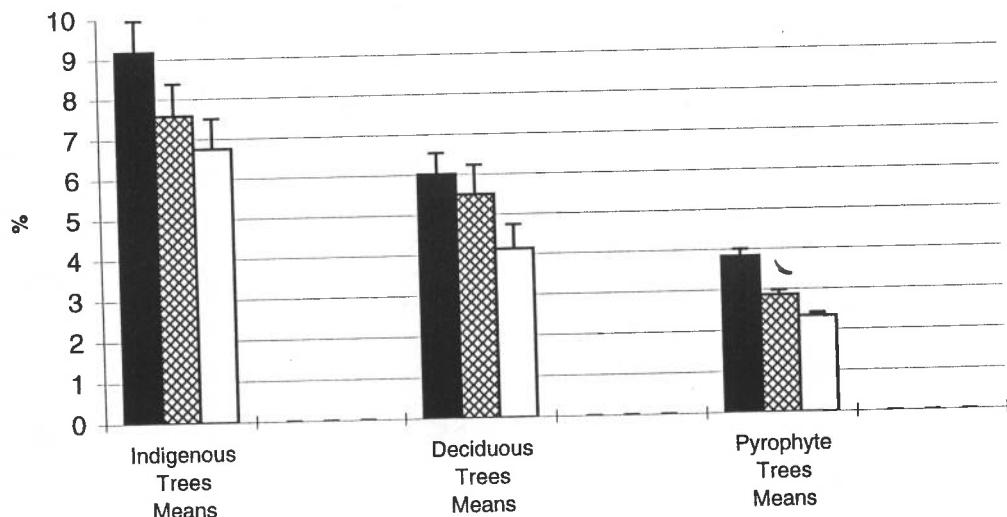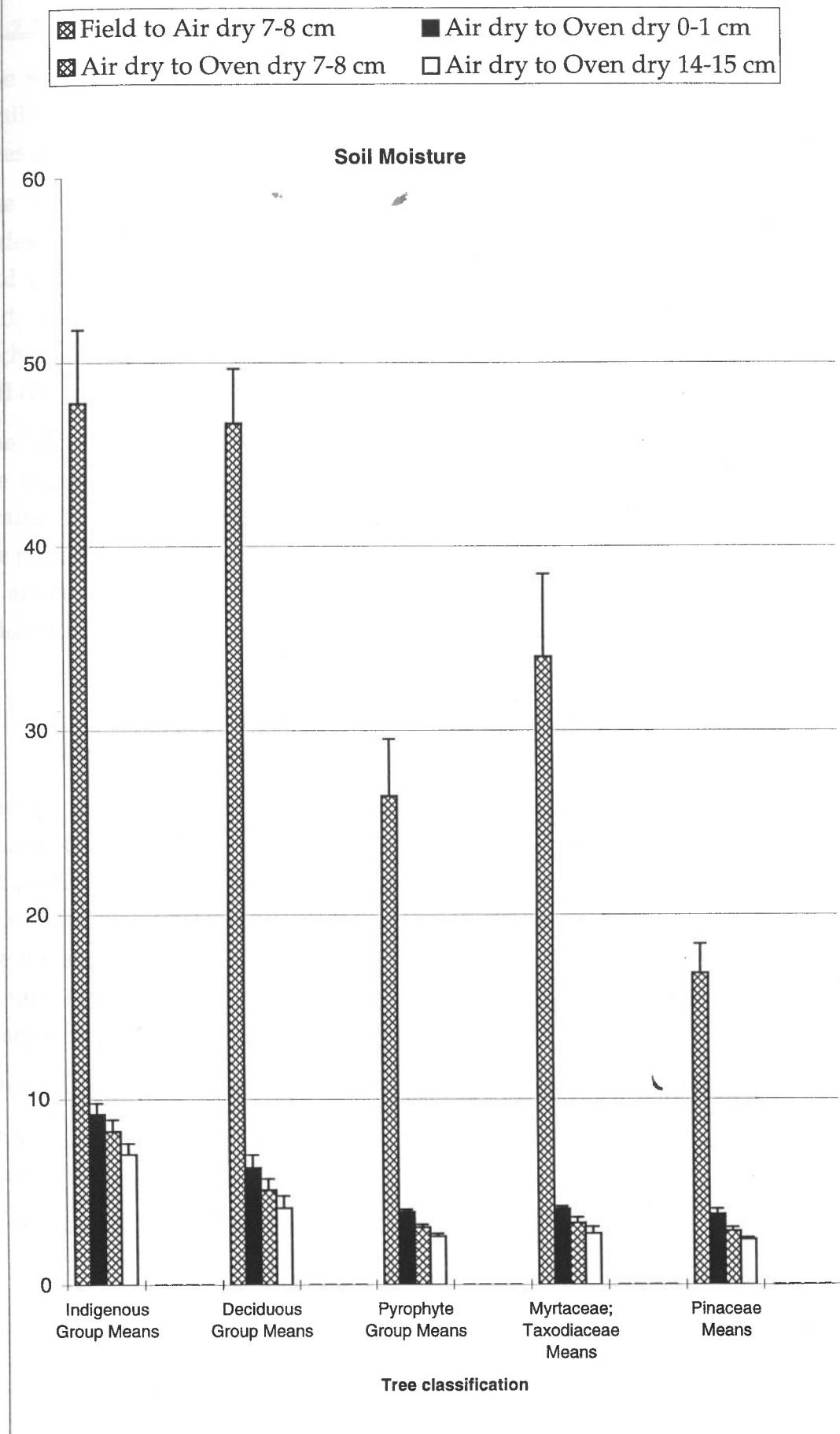
6.4.2.2.c;   Total exchangeable bases (Fig. 6.4.1.c).

The soil A-horizon amounts of total exchangeable bases are indicative of the site fertility and of the nutrient cycling and nutrient storage strategy of the particular trees and associated biota.

The T.E.B. values of the soil B and C horizons from the Dunedin and Warepa soil series ranged between 0.7 and 5.5 me % (Tomlinson and Leslie, 1977). **Indigenous and exotic deciduous trees** demonstrate soil A-horizons base cation incorporation and **effective nutrient cycling and storage tendencies**. The amounts of exchangeable bases in the soil A-horizon increases three to ten fold with decreasing soil depth under these associations.

The T.E.B. means in the soil A-horizon of the pyrophanerophyte group are within the range of the mineral substrate. This indicates that any minerals that are made available through plant induced increases of mineral weathering are immobilized in the biomass of the tree. The addition of firetree litter to the mineral soil does not lead to an increase of the total exchangeable cations, but to the formation of organic, acidic leachates, which encourage the weathering of minerals.

> **The data presents no indication of nutrient cycling under firetrees.** The lower soil depths show very low T.E.B. values and standard errors, which support the concept of a common firetree strategy of soil nutrient extraction.

The dendrogram based chart on the **exchangeable bases (Fig. 6.4.2.c)** demonstrates clearly the effects of the grouping of trees with respect to the dendrogram tree classification. The differences between "indigenous" and "deciduous" groups are accentuated and the standard errors are lowered. The "pyrophanerophyte" means are substantially lower, than those of either the "indigenous" or the "deciduous" group. The *Pinaceae* means demonstrate substantially lower means of exchangeable bases, compared with the myrtax group.

The typical chart displays highest to lowest means in the following order:

"indigenous" group > "deciduous" group > myrtax group > "pyrophanerophyte" group > Pinaceae; and

upper soil level > mid soil level > lowest soil level.

This same pattern occurs between tree groups for the following soil parameters:

C.E.C. (Figs. 6.4.2.d); base saturation (Figs. 6.4.2.e); calcium (Figs. 6.4.2.f); potassium (Figs. 6.4.2.g); phosphorus (Figs. 6.4.2.n); soil organic matter (Figs. 6.4.2.j); carbon (Figs. 6.4.2.k); nitrogen (Figs. 6.4.2.l).

FIGURE: 6.4.1.c

TOTAL EXCHANGEABLE BASES

■ 0 - 1 cm ▨ 7 - 8 cm □ 14 - 15 cm

mineral T.E.B. 0.7 - 5.5 me%
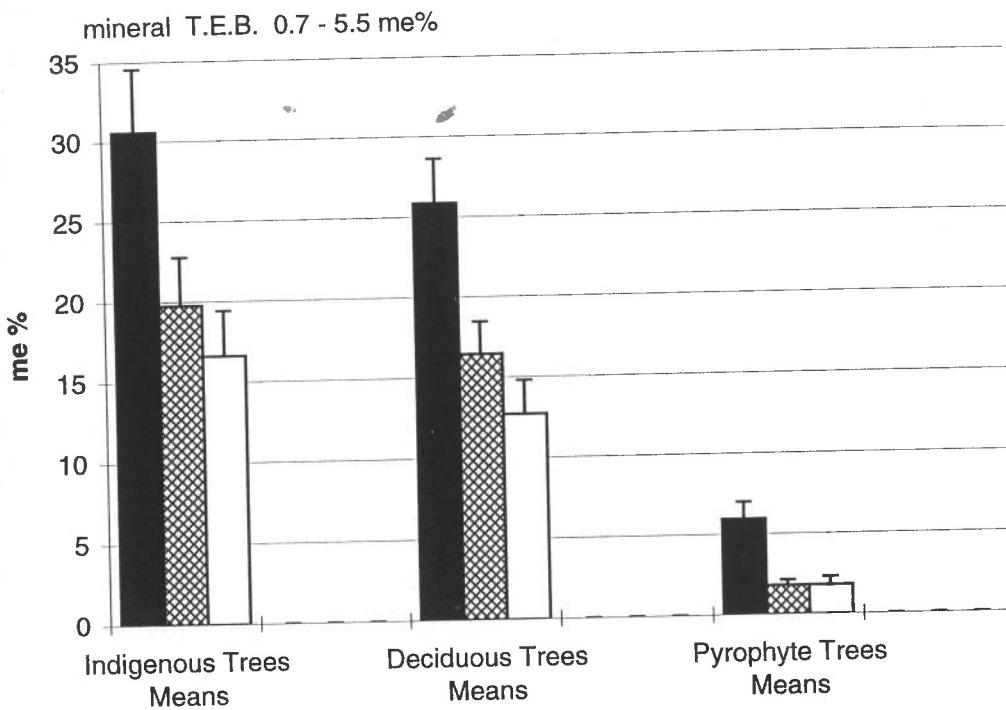
FIGURE: 6.4.2.c

Total Exchangeable Bases

■ 0 - 1 cm ▨ 7 - 8 cm □ 14 - 15 cm
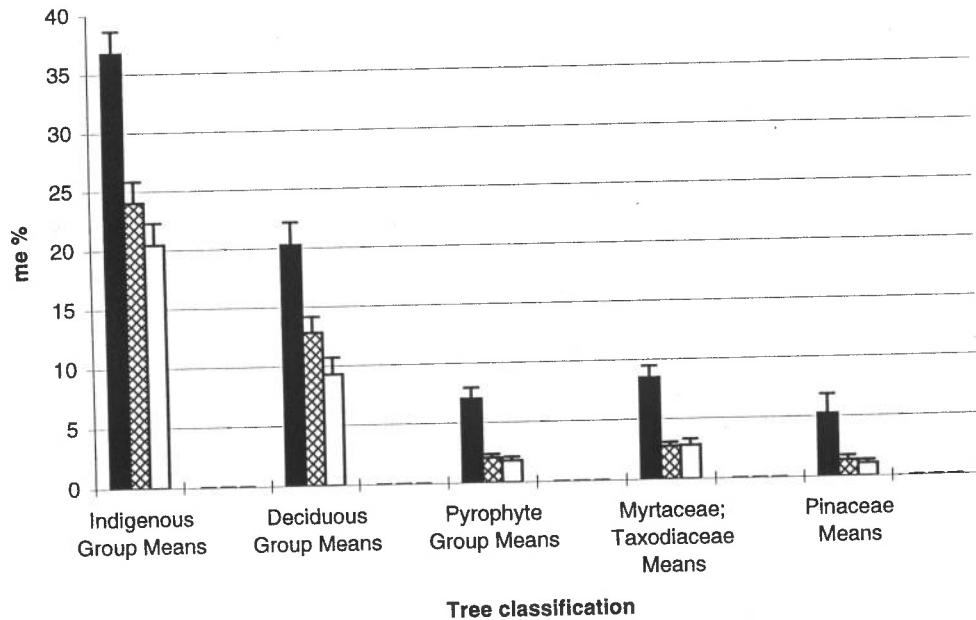
6.4.1.2.d: Cation exchange capacity (Fig. 6.4.1.d).

A comparison of the cation exchange measurements offers interesting information with regard to the relative increases of cation exchange sites on organic material under various trees and at various soil depths.

The mineral exchange capacity for the soil series ranges between 14 and 16 me % (Tomlinson and Leslie, 1978). The three to fourfold increase of the C.E.C. under indigenous and exotic deciduous trees is indicative of active bioturbation and the incorporation of organic exchange sites into the soil A-horizon.

The pyrophanerophyte group shows an increased C.E.C. at the upper soil strata and little differences to the mineral C.E.C. at both of the lower soil depths. This steep reduction indicates a lack of both, bioturbation and incorporation of exchange sites on organic matter in the mineral matrix under firetrees. The standard errors are small, indicating a common firetree response.

The indigenous myrtaceous *Kunzea ericoides* maintains a doubling of the mineral C.E.C. at the lower soil levels (Appendix: B; Table 2).

FIGURE: 6.4.1.d

CATION EXCHANGE CAPACITY
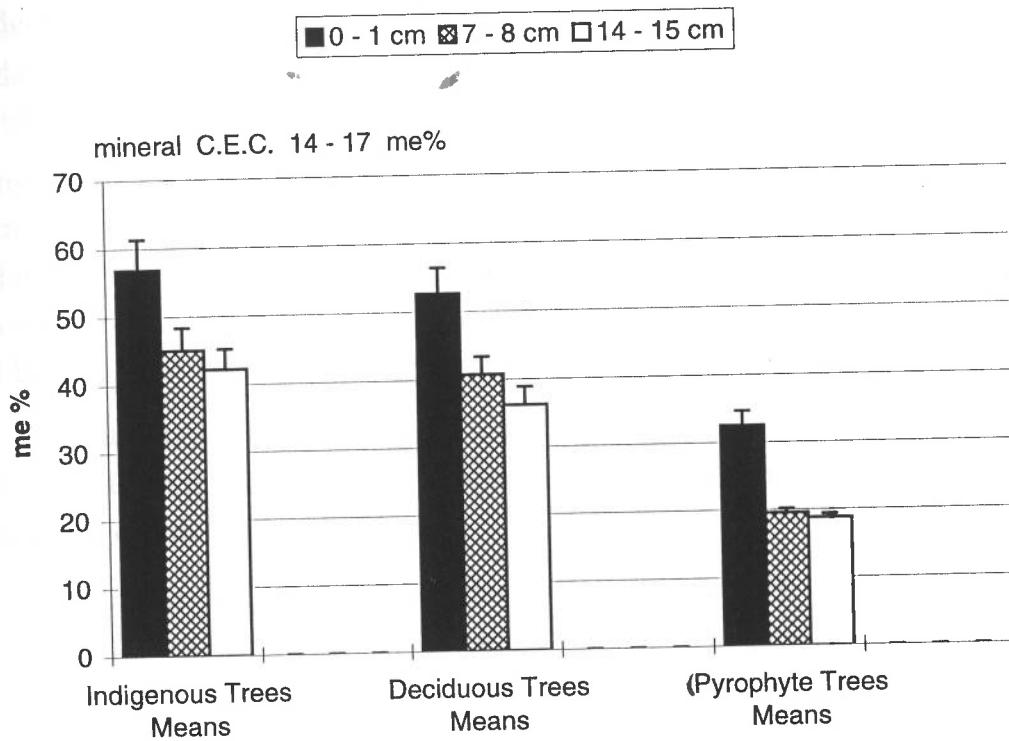
FIGURE: 6.4.2.d

Cation Exchange Capacity
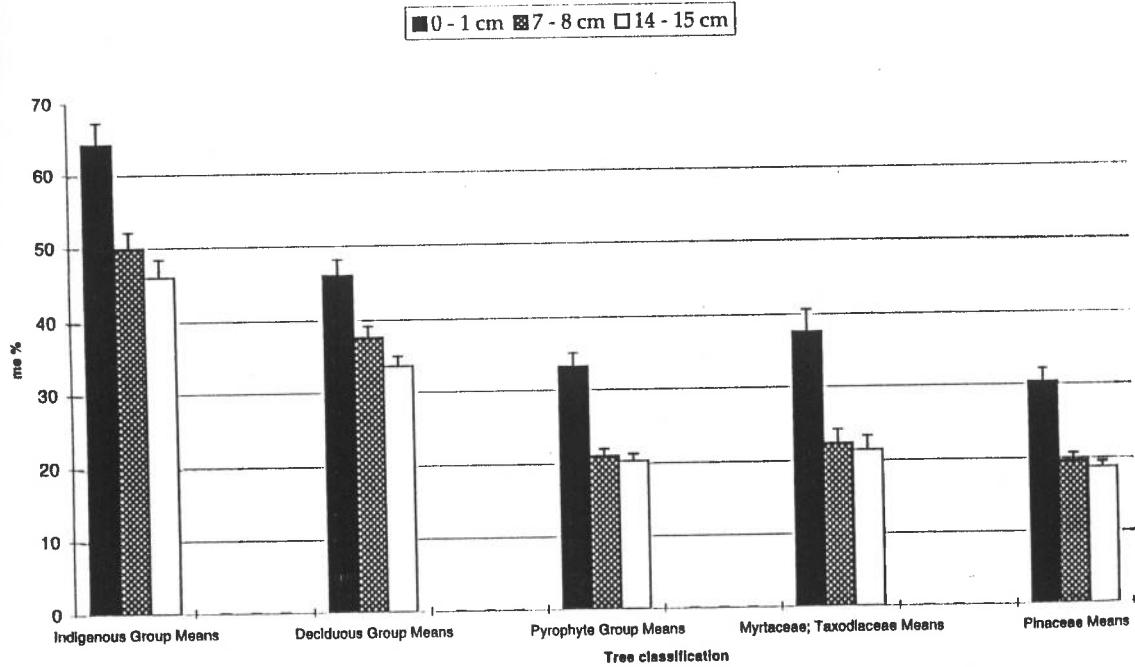
6.4.1.2.e: Base saturation (Fig. 6.4.1.e).

Similarly the percentages of base saturation differ markedly and vary from averages of 53% to 33% from the upper to the lowest soil level of the indigenous trees and the exotic deciduous angiosperms, to base saturations of 21 % to 5 % amongst the eucalypts and gymnosperms. The averages are decreasing with depth for all tree groups (Appendix: B; Table 2).

The mineral base saturation ranged between 4 and 33 % (Tomlinson; Leslie, 1977). The addition of organic material and associated increases in C.E.C., and the cycling of nutrients under both groups of indigenous and exotic deciduous angiosperms leads to an increase of the base saturation with decreasing soil depth and exceeds the mineral base saturation at all soil depths.

A very different trend can be observed under the pyrophaneraophytes. The base saturation is within the range of the mineral base saturation at all depths, and lowest at the mid-soil depth of 7 - 8 cm.

These results again support the suggestions made above, with regard to the predominance of nutrient extraction under pyrophanerophytes.

FIGURE: 6.4.1.e

Base Saturation

mineral B.S. 4 - 33%
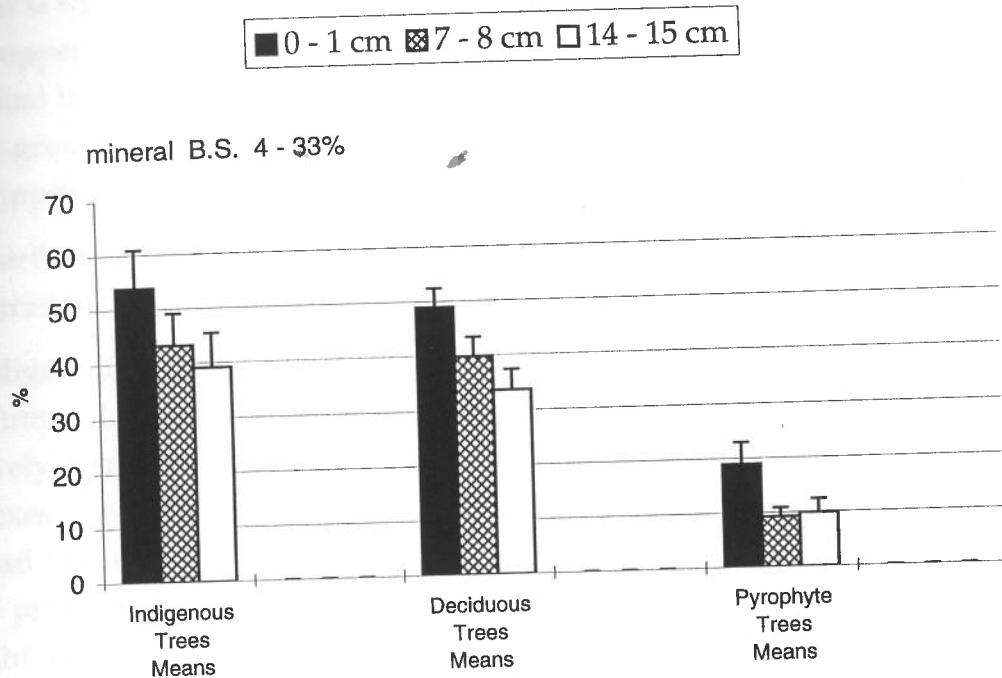
FIGURE: 6.4.2.e

Base Saturation
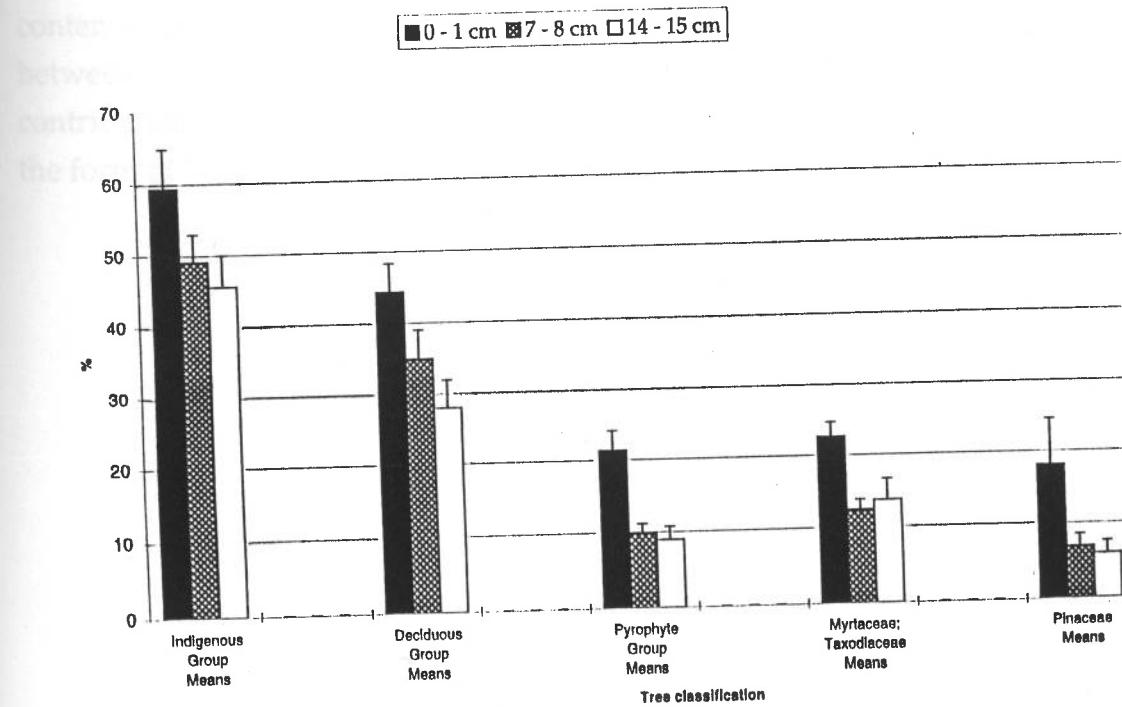
6.4.1.2.f,g: Calcium and Potassium (Fig. 6.4.1.f,g).

Calcium is by far the most abundant cation and its distribution is generally highest in the upper most soil level and decreasing with depth. The variability between individual trees is high and there are immense differences between the averages of the two groups of gymnosperms and eucalypts and indigenous and exotic deciduous trees (Appendix: B; Table 2).

The distribution of potassium exhibits a similar tendency at a fraction of the Ca concentrations (Appendix: B; Table 2).

The indigenous trees and the exotic deciduous trees show amounts of calcium and potassium, which substantially exceed those of the mineral contribution and are negatively correlated with soil depth. This points to the formation of organo-mineral complexes (Ca-humates) (Kononova, 1966) in the soil A-horizon, generated by a litterload and throughfall, which is rich in mineral cations and organic composites. (Ca is predominantly incorporated in the litter and K frequently derives from throughfall),. Calcium contents of leaf litter increase with leaf age, since calcium can not be relocated and cycled internally. Therefore calcium is the major cation involved in the organo-mineral cycle and functions as an alcaline conditioner of potentially acidic organic complexes in the soil medium. The organo-mineral combinations are readily decomposable and cyclable (Stevenson, 1982; 1986).

However, the amounts of calcium under pyrophanerophytes are within the range of the mineral contents at all soil depths and substantially less than the soil-calcium contents under the other tree-groups. A similarly contrasting relationship exists between tree-groups for the soil K contents. Slight increases of K, above the mineral contribution are indicative of limited K input under pyrophanerophytes, possibly in the form of leachate losses from leaves.

FIGURE: 6.4.1.f

Calcium

■ 0 - 1 cm   ▨ 7 - 8 cm   ☐ 14 - 15 cm

mineral Ca 0.2 - 3 me%
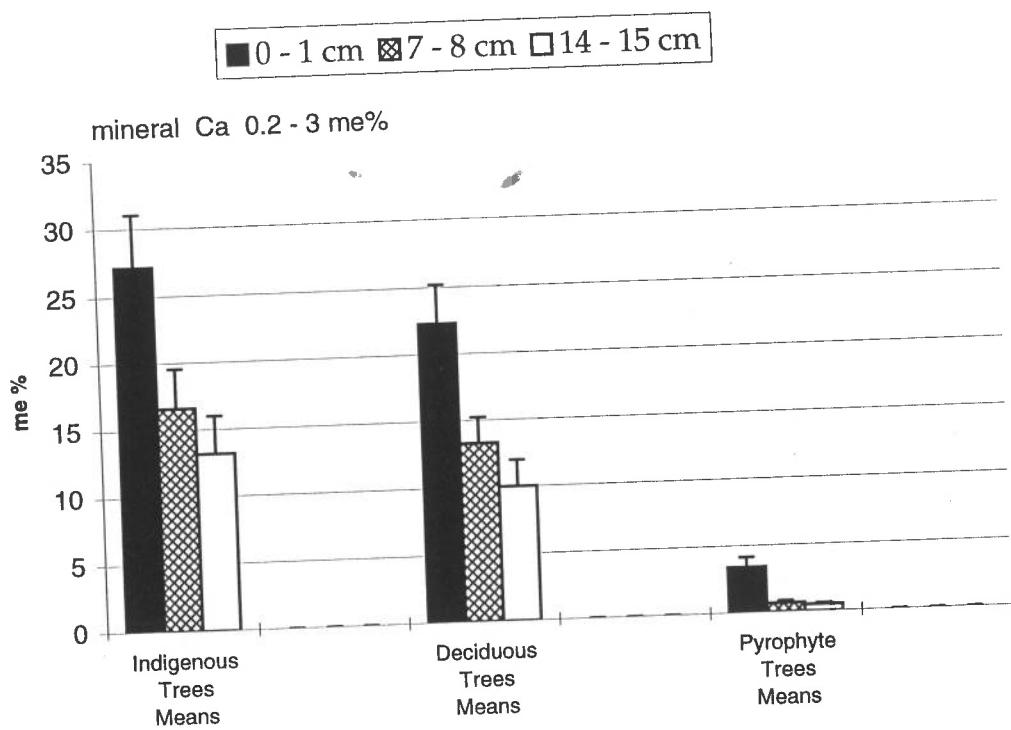
FIGURE: 6.4.2.f

Calcium

■ 0 - 1 cm   ▨ 7 - 8 cm   ☐ 14 - 15 cm
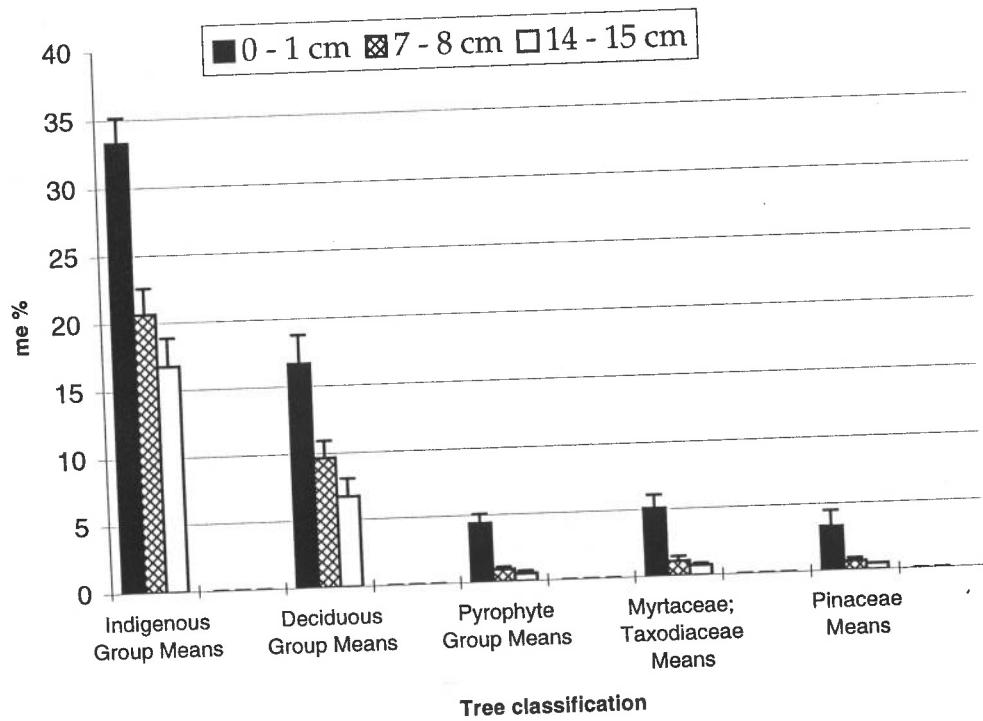
FIGURE: 6.4.1.g

Potassium
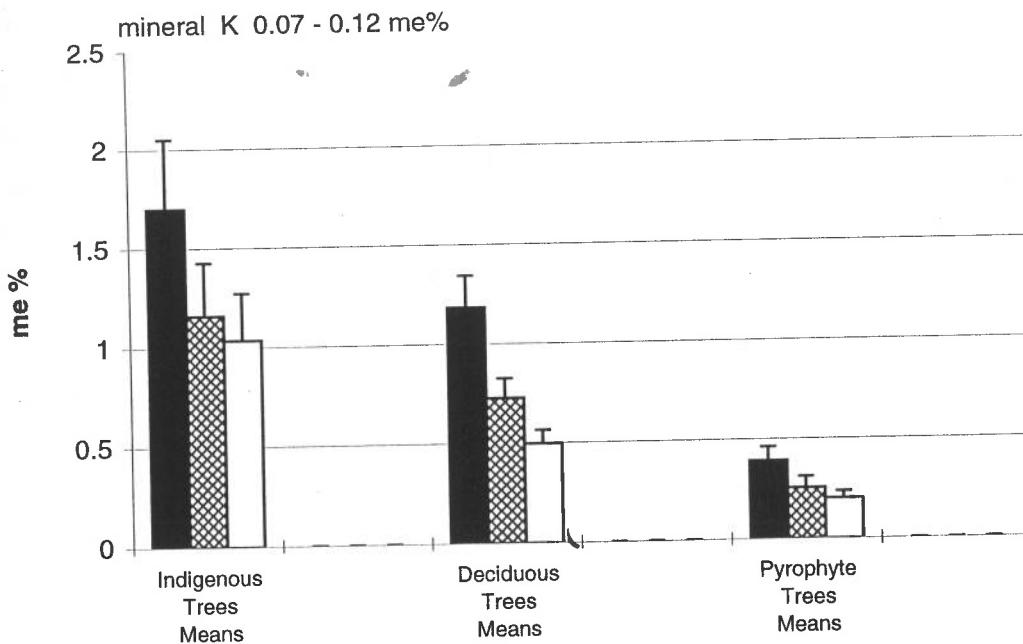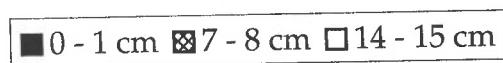
FIGURE: 6.4.2.g

K ; Potassium
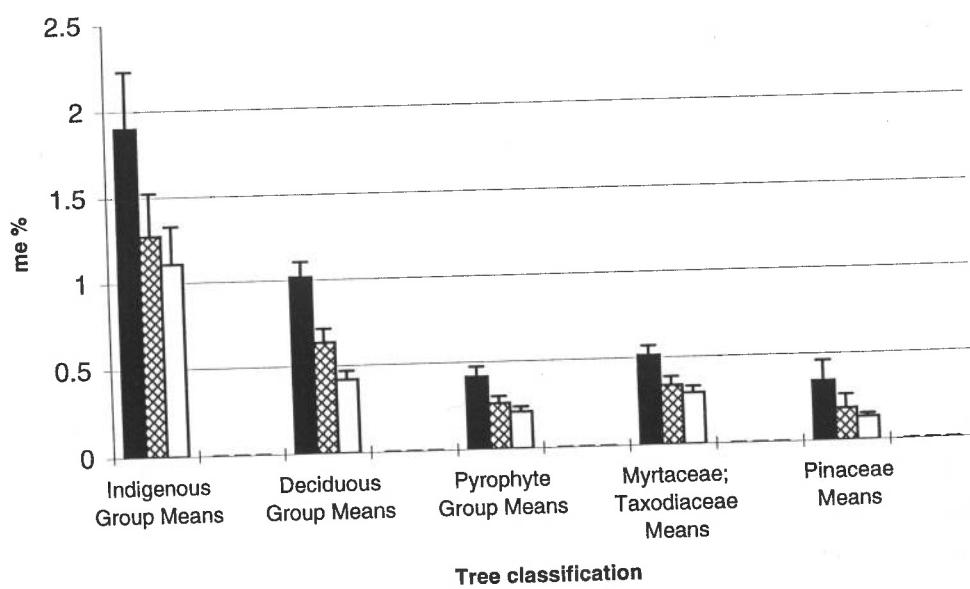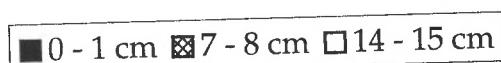
6.4.1.2.h.i: Magnesium and Sodium (Fig. 6.4.1.h,i).

The distribution of magnesium follows a different pattern under <u>indigenous trees</u> and <u>exotic deciduous angiosperms</u>. Both vegetation types feature higher amounts of magnesium at the lower soil levels.

However, the distribution of magnesium in the soil levels appears to be rather individual and some trees like *Dacrydium cupressinum*, *Kunzea ericoides* and *Fagus sylvatica* display decreasing amounts of magnesium with depth.. The same trend is apparent under <u>eucalypts</u> and <u>gymnosperms</u> (Appendix: B; Table 2).

The distribution of sodium is rather irregular. The highest concentrations can most frequently be found in the lowest and the upper most soil level (Appendix: B).

The range of the soil series' mineral contents of magnesium is slightly less and lies within that of calcium. There are however interesting differences with regard to the cycling dynamics of magnesium under the influence of the three tree associations and depth levels, which is unlike that of both Ca and K.

The magnesium contents of the soil A-horizon are generally within the range of the mineral contents.

The magnesium contents increase with depth under the indigenous trees. The upper most soil level has the lowest magnesium contents of all groups, indicating that the investigated indigenous trees might be effective in the relocation of magnesium prior to abscission and that consequently the litter contains limited amounts of magnesium. Under the examined exotic deciduous trees the magnesium contents are high at all soil depths and particularly at the mid soil level, indicating that magnesium is cycled and accumulated in the soil A-horizon. Contrary to calcium, magnesium is relocated prior to abscission and cycled within the tree. The autumnal colouring of the leaves provides visible evidence.

The group of pyrophanerophytes shows different magnesium cycling tendencies. High amounts at the upper soil level contrast with low amounts at both of the lower soil depths. Magnesium cycling within the trees and via the organic mineral soil seems to be less effective.

Sodium is the least abundant, the smallest in size and potential and hence the most mobile cation. These physical facts are reflected in the distribution of Na at the soil depth levels under all tree associations. Na levels are higher at the lowest soil depth level, compared to the mid soil depth level under all tree associations. Na seems to be retained and cycled most effectively under the indigenous trees. The mineral

range for sodium is exceeded at all soil depth levels under indigenous trees, only at the upper soil level under the exotic deciduous group, and only at the lowest soil depth level under the pyrophanerophyte group.

Soil **magnesium** and **sodium** (6.4.2.h; 6.4.2.I) contents of the dendrogram grouping differ from the above mentioned soil parameters Ca and K (6.4.2.f; 6.4.2.g). Highest overall amounts of **magnesium** are found under the trees of the "deciduous" group. Within the "deciduous" group the mid soil level shows the highest means and the lowest standard errors. This possibly correlates to high amounts of humic acid at this soil depth under the deciduous trees.

The myrtax group demonstrates the highest absolute level of magnesium at the upper soil horizon and a considerable decrease with soil depth. This trend is repeated, but with lower means under the *Pinaceae*.

Under the trees of the "indigenous" group, however, Mg increases with soil depth. This indicates either a high magnesium retention in the standing biomass or an efficient immobilization by the decomposer community.

The highest amounts of **sodium (Fig. 6.4.2.i)** are typically found at the lowest soil depth level and the lowest amounts at the mid soil depth level under most groups.

Two high standard errors at the upper soil level in the "deciduous" group and at the lowest soil level of the myrtax group point to the possibility of local salt contamination or errors of other origin.

Sodium cycling is indicated by high depositions of sodium under indigenous and deciduous trees. Under all trees a depletion of exchangeable sodium at the mid soil level, could be indicative of either its high mobility in the soil solution, caused by its physical (relatively small size) and chemical (low valency) characteristics or of biological processes that lead to the immobilisation of sodium. The lowest soil level shows high values of exchangeable sodium under the trees of the "indigenous" group and the myrtax group.

FIGURE: 6.4.1.h

Magnesium
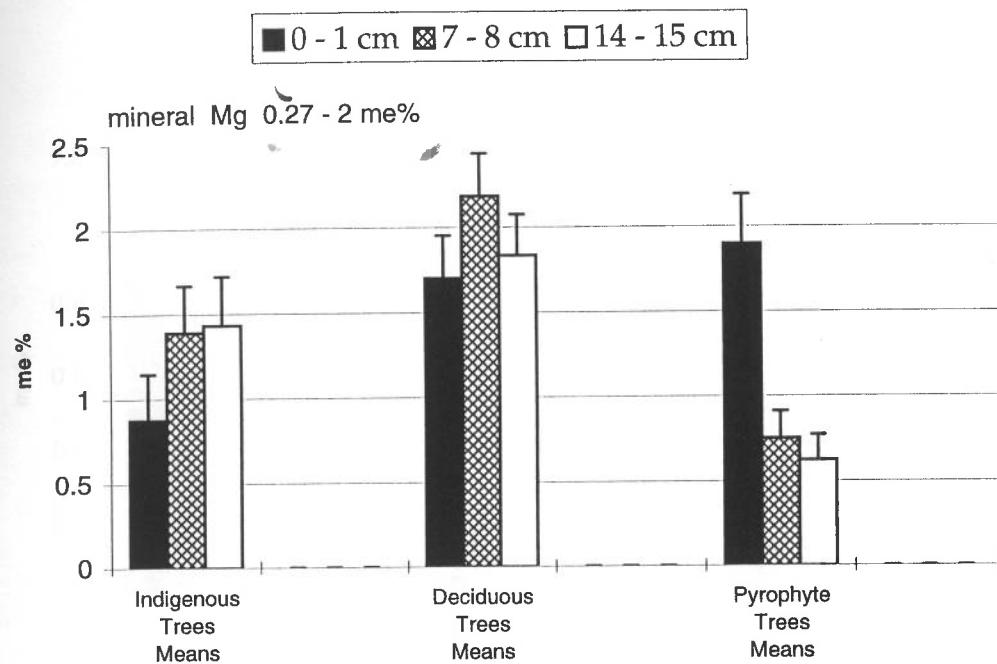
FIGURE: 6.4.2.h

Magnesium

FIGURE: 6.4.1.i

Sodium

FIGURE: 6.4.2.i

Na ; Sodium
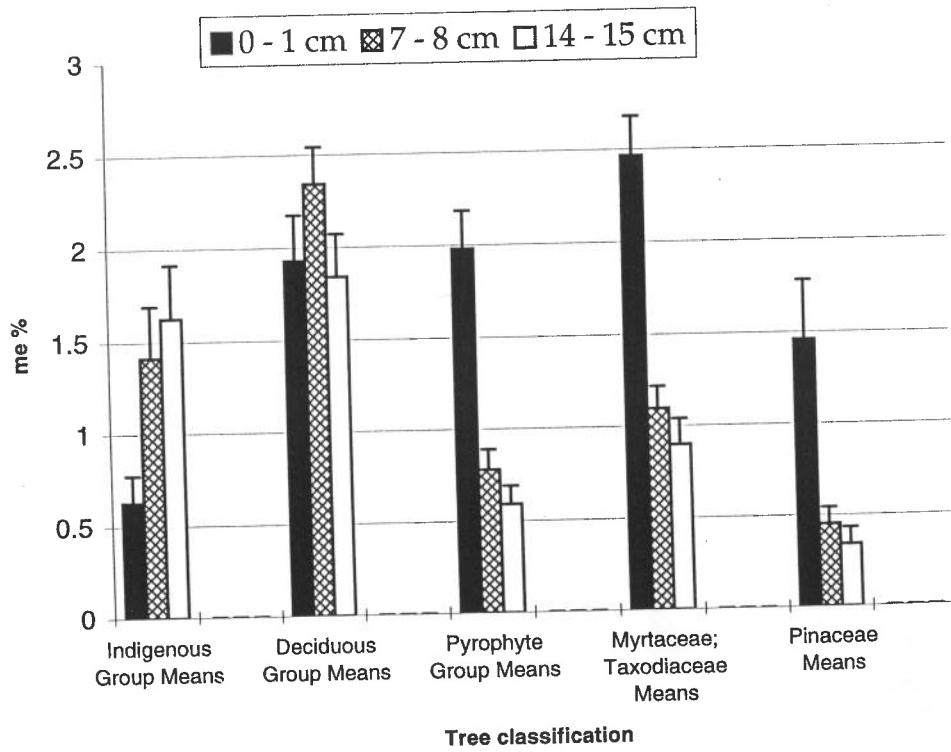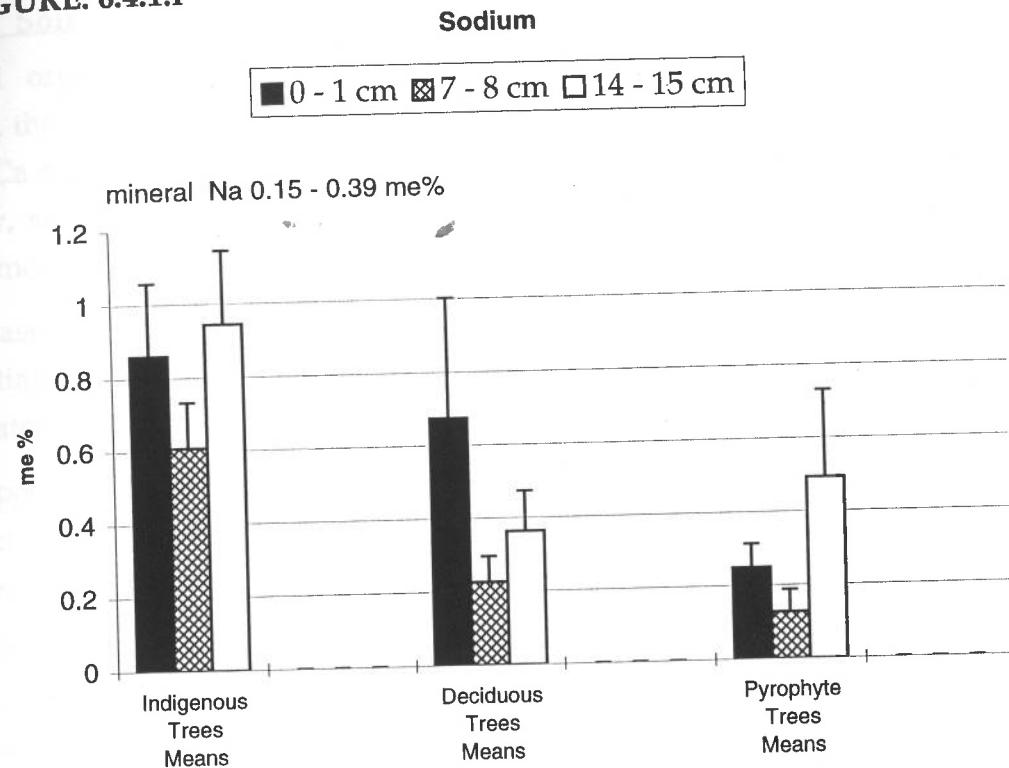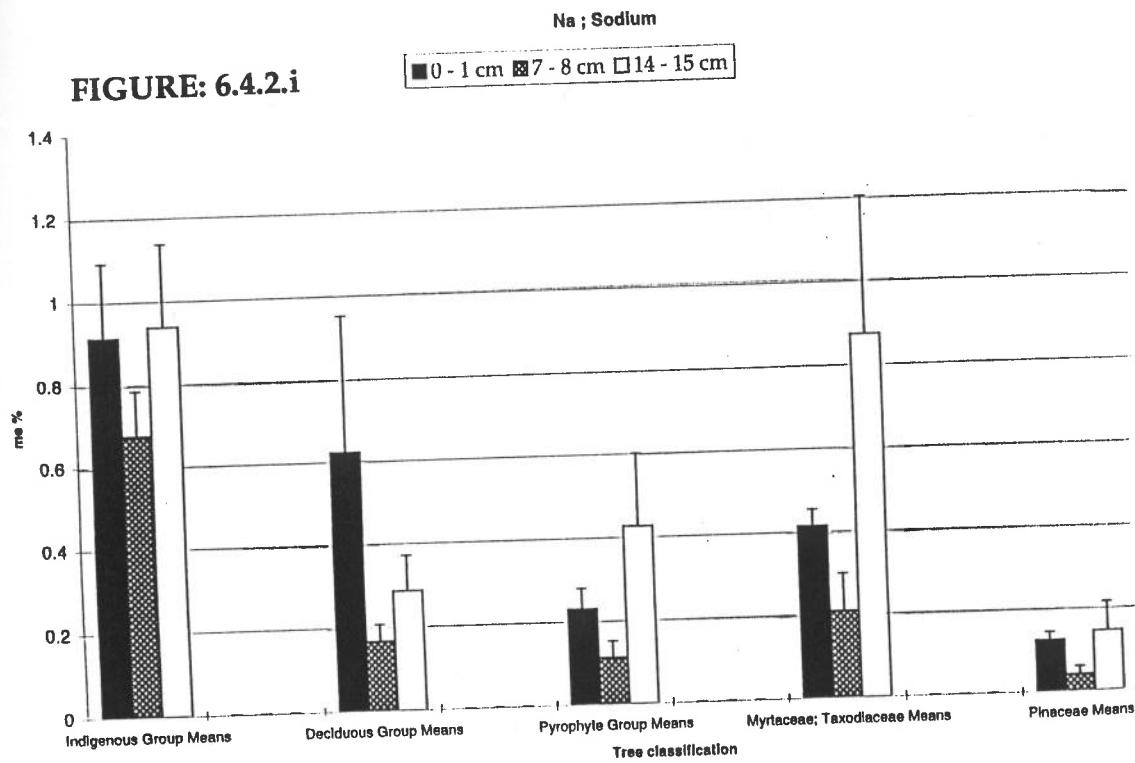
6.4.1.2.j: Soil organic matter (Fig. 6.4.1.j).

The soil organic matter (s.o.m.) component includes semi-decomposed plant material, the relatively stable humic fractions, a variety of minor carbon compounds such as Ca carbonates, as well as the soil fauna and flora. Because of this component diversity, s.o.m. can only be used as a crude estimate for the recognition of soil developmental trends.

A decrease of soil organic matter with soil depth is common to all tree groups. Substantial amounts of soil organic matter from the upper soil level are derived from plant material in various stages of decompostion.

The upper soil level contains the highest amounts of s.o.m. at all sample sites. However, at the lower soil levels the group differences are more pronounced. The amounts vary considerably from one tree to the other, within groups.

Field- observations indicate that the soil meso- and macro fauna is less numerous under the gymnosperms and eucalypts and the low s.o.m. percentages in the mineral soil give an indication that the soil biota is less effective in the mixing of plant residues with the mineral soil. This observation is confirmed by published research (Kononova, 1966; Swift et al., 1979; Stevenson, 1982, 85).

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FIGURE: 6.4.1.j

Soil Organic Matter

■ 0 - 1 cm ▨ 7 - 8 cm ☐ 14 - 15 cm
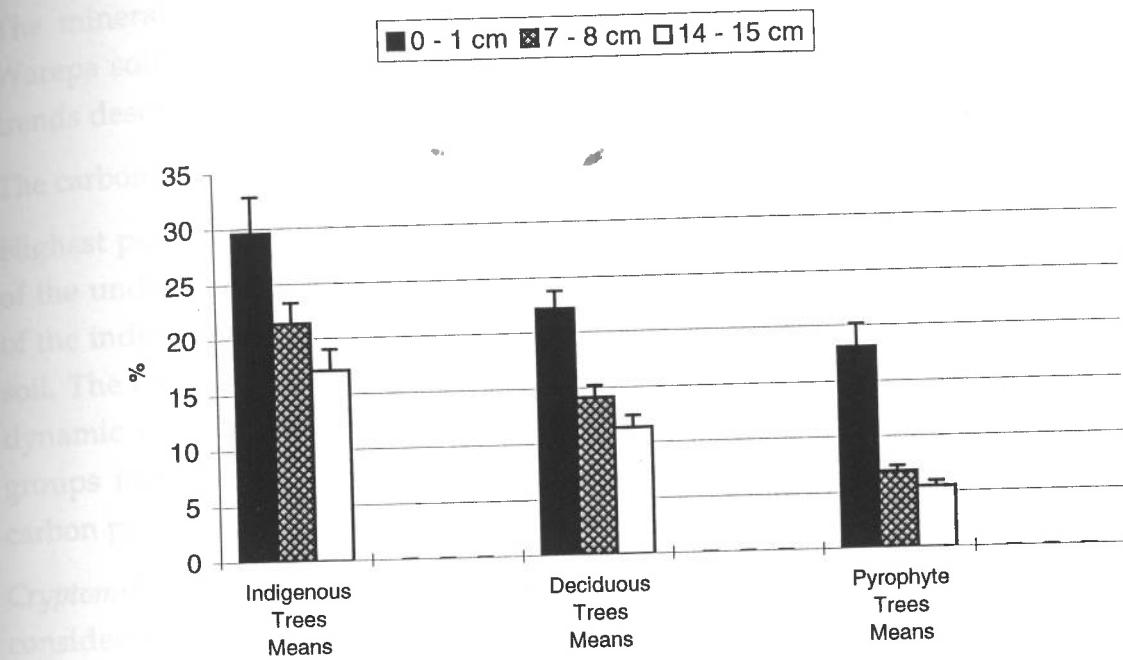
FIGURE: 6.4.2.j

Soil Organic Matter

■ 0 - 1 cm ▨ 7 - 8 cm ☐ 14 - 15 cm

Tree classification
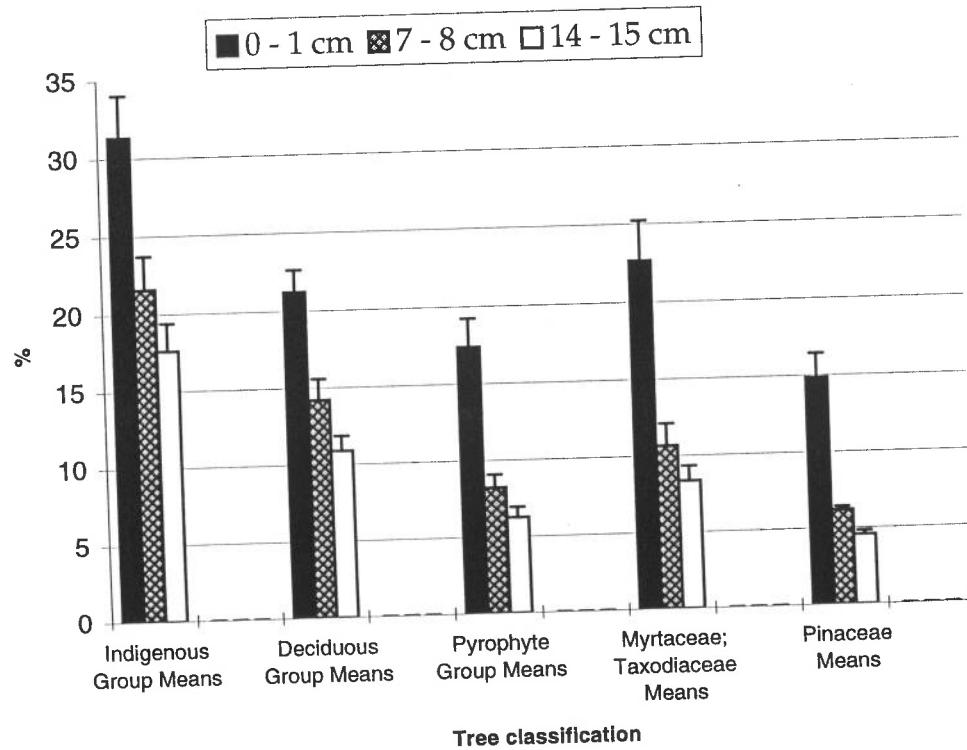
6.4.1.2.k: Soil carbon (Fig. 6.4.1.k).

The mineral carbon contents range between 0.4 and 1.3 % in the Dunedin and Warepa soil series (Tomlinson, Leslie, 1987). Soil carbon contents largely reflect the trends described for the C.E.C.

The carbon concentrations are generally decreasing with soil depth.

Highest percentages of carbon are found under the indigenous trees. The influence of the undisturbed site under the *Podocarpaceae* is visible from the high error values of the indigenous group. Logging had never removed the biomass and exposed the soil. The carbon contents of the soil could accumulate and be maintained at a high dynamic equilibrium. Individual variations within the indigenous and deciduous groups indicate the individual variability of nutrient cycling strategies. High soil carbon percentages are found for example under *Nothofagus* species.

Cryptomeria japonica and *Acacia melanoxylon* display carbon values, which are considerably higher, especially at the lower soil levels, when compared to the *Pinaceae* and *Eucalyptus regnans* (Appendix: B).

FIGURE: 6.4.1.k

CARBON

■ 0 - 1 cm ▨ 7 - 8 cm ☐ 14 - 15 cm

mineral C 0.4 - 1.3 %
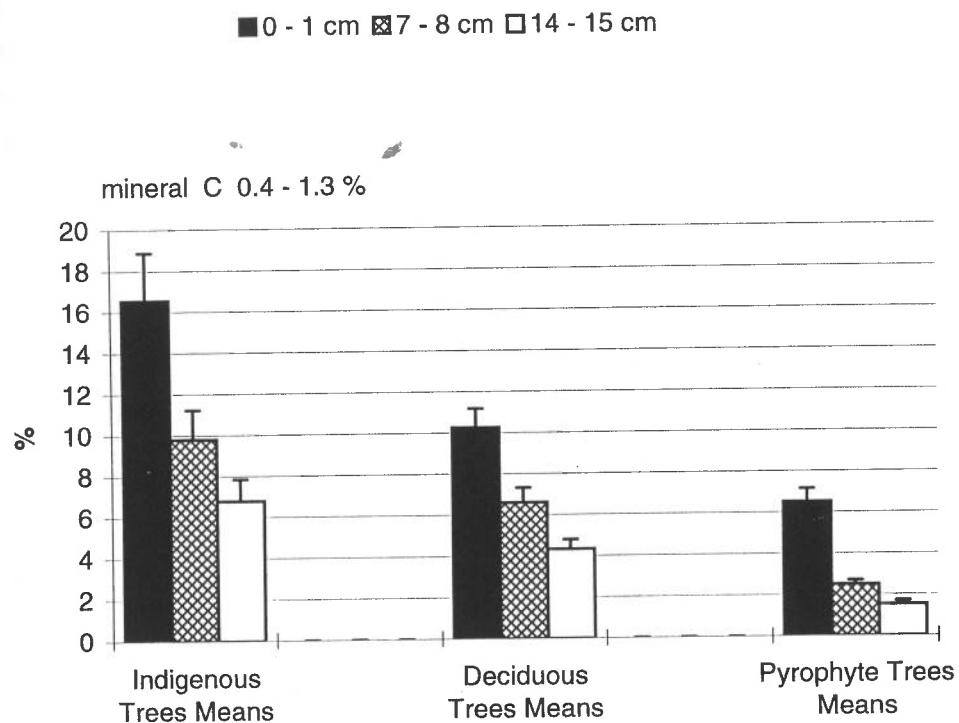
FIGURE: 6.4.2.k

Carbon

■ 0 - 1 cm ▨ 7 - 8 cm ☐ 14 - 15 cm
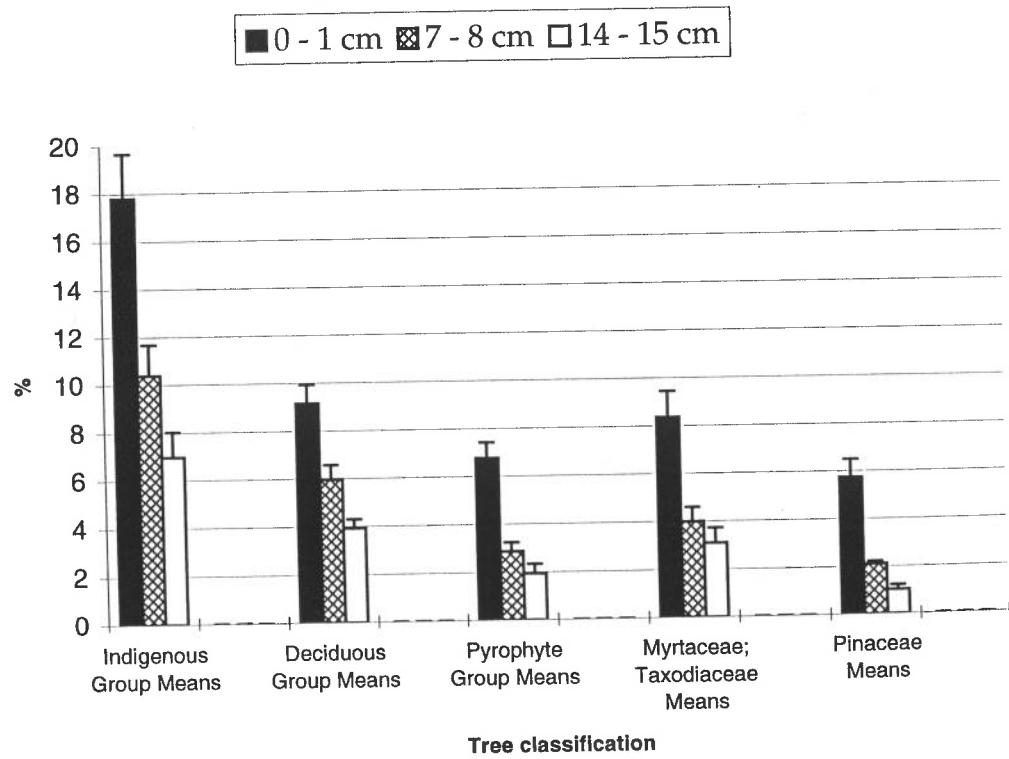
6.4.1.2.1: Soil nitrogen (Figure 6.4.1.1).

The mineral contribution ranges between 0.04 to 0.08% (Tomlinson, Leslie, 1978). Highest means are reached at the uppermost soil level under exotic deciduous trees. Both indigenous and exotic deciduous groups clearly show nitrogen storage increases in the mineral soil.

The means for the pyrophanerophytes again are within the mineral range at the lower two soil depths and only slightly exceed the mineral N levels at the uppermost soil level. The means and error values of the fire trees support the suggestions made in relation with the other soil parameters, such as pH; T.E.B., C.E.C.

Nitrogen is plant available in anionic (NO^{3-}) and cationic (NH^{4+}) form.

Since nitrogen is a prerequisite of the synthesis of protein these substantial differences are indicative of substantial differences in the soil biota underneath individual trees.

FIGURE: 6.4.1.1

NITROGEN

■ 0 - 1 cm ▨ 7 - 8 cm □ 14 - 15 cm

mineral N 0.04 - 0.08 %
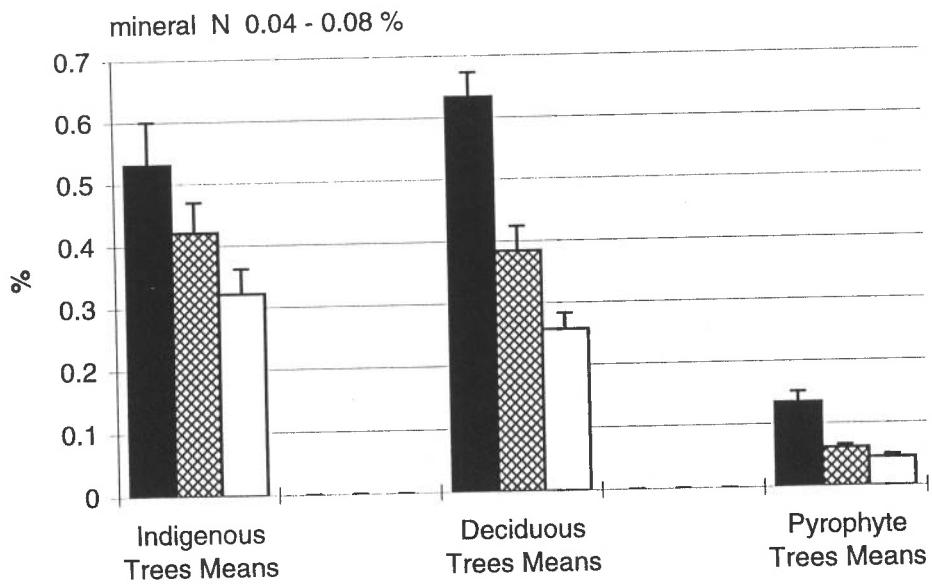
FIGURE: 6.4.2.1

Nitrogen

■ 0 - 1 cm ▨ 7 - 8 cm □ 14 - 15 cm

Tree classification
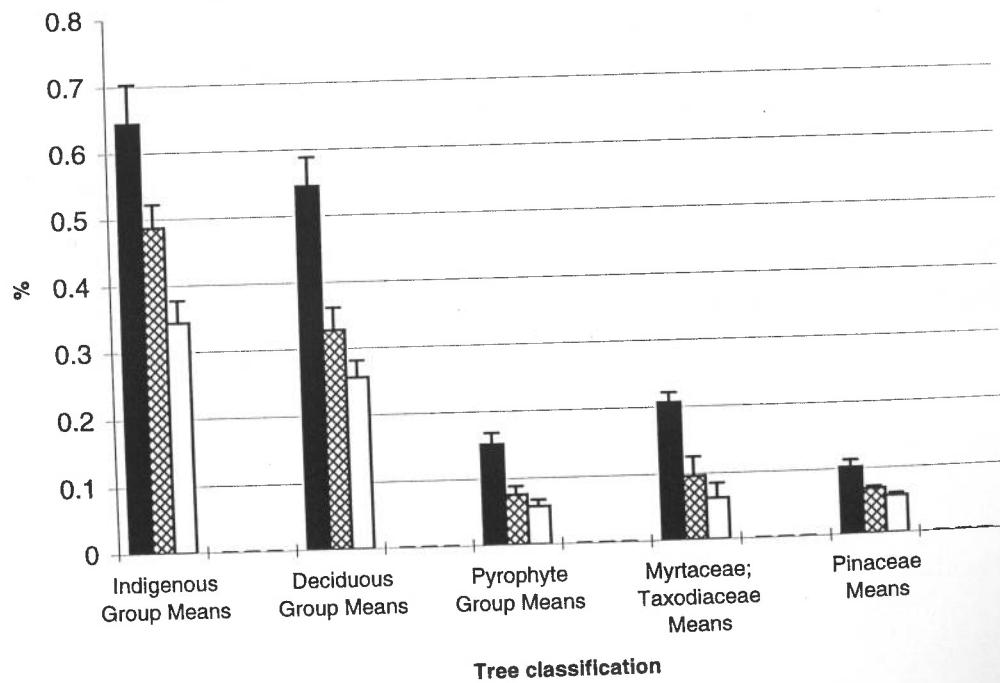
6.4.1.2.m; Elemental Ratio: Carbon to Nitrogen (Fig. 6.4.1.m).

The ratio of carbon to nitrogen is a very important indicator of soil fertility.

A low ratio encourages the synthesis of protein and soil biotic activities are facilitated, whereas a high ratio has an inhibitive effect on the soil microbes and the decomposability of plant material.

At C/N ratios of < 20 a net mineralization of (NH^{4+} and NO^{3-}) occurs and exchangeable mineral nutrients will be gained in the soil solution.

A net immobilization (loss) of N will occur at C/N ratios of > 30.

An intermediate ratio leads to neither gain nor loss of N (Stevenson, 1986).

This ratio relates to certain soil humus types under the tree groups.

A C/N ratio of 50 under the fire trees indicates the development of a mor humus type, with net N immobilization.

The indigenous trees together develop a moder humus type at a C/N ratio of between 20 and 30. The individual differences are however substantial, with high C/N ratios for the genus *Nothofagus* at the upper soil strata, and around 20 at the mid- and lowest soil strata (Appendix: B; 2).

The exotic deciduous trees indicate the development of a most favourable mull humus type, with C/N ratios between 10 and 20 at all soil depths and little variation between species (Stevenson, 1982; 1986; Schroeder, 1983). This implies that nutrients are accumulating under deciduous trees.

The three distinct soil humus types (mull; moder; mor) are associated with different combinations of humic matter fractions, distinct humic morphological structure, as well as a divergent soil depth distribution of the humic matter fractions (Kononova, 1966; Swift, 1979; Stevenson 1982).

The soil humus types are reported to be analogous with various vegetation compositions in the temperate humid biome and represent soil fertility levels and - potentials (Schroeder, 1983).

FIGURE: 6.4.1.m

RATIO CARBON / NITROGEN

■ 0 - 1 cm ▨ 7 - 8 cm ☐ 14 - 15 cm

mineral C/N 10 - 16
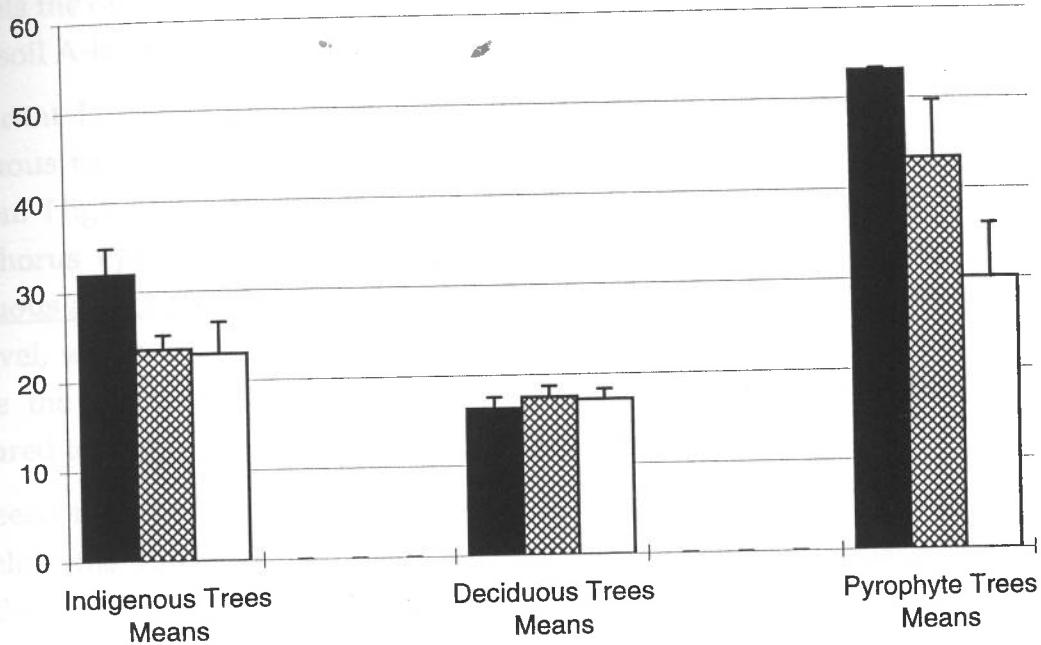
FIGURE: 6.4.2.m

Ratio: Carbon / Nitrogen

■ 0 - 1 cm ▨ 7 - 8 cm ☐ 14 - 15 cm

Tree classification
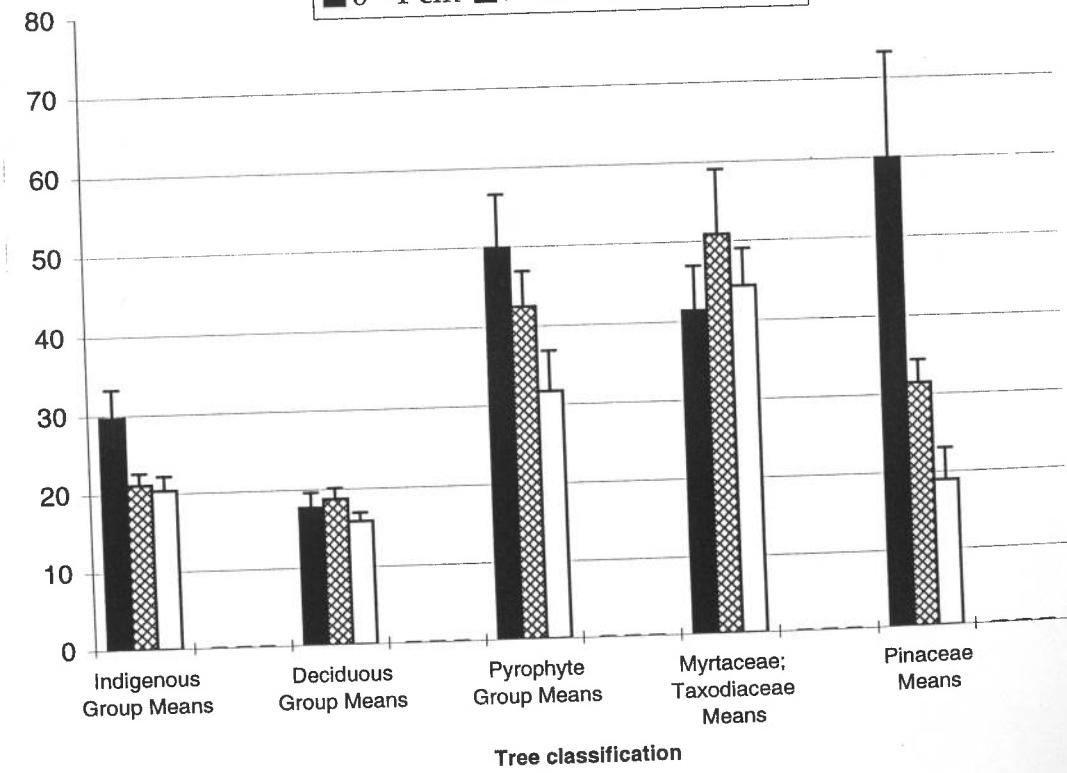
6.4.1.2n: Phosphorus (Fig. 6.4.1.n).

Only a very limited supply of plant available phosphorus (4.6 - 5.5.mg/Kg) is present in the mineral soil (Tomlinson, Leslie, 1978). Available soil phosphorus parallels the observations on other soil parameters, with regard to storage tendencies in the soil A-horizon.

Significant increases of available phosphorus under both indigenous and exotic deciduous trees show that phosphorus is cycled and incorporated into the soil A-horizon. High standard errors under indigenous trees indicate strong individual phosphorus cycling variations between species. The indigenous trees and exotic deciduous angiosperms accumulate substantial amounts of phosphorus in the upper soil level, which were in excess of 20 mg P / kg for some trees. There are double to tripple the amounts of soil phosphorus under indigenous and deciduous trees compared to gymnosperms and eucalypts (Appendix: B; Table 2).

Firetrees, on the other hand demonstrate values of phosphorus at all soil depths that are below the values measured for the mineral contribution. This is in agreement with the previously discussed observations (exchangeable bases) with regard to the nutrient extraction strategies of firetrees.

Phosphorus occurs as an exchangeable anion in conjunction with oxygen in the soil in the following configurations $H_2PO_4^-$, HPO_4^{2-}, (PO_4^{3-}). Plant uptake of phosphorus seems to be largely dependent on the weathering processes in the mineral soil (Stevenson, 1986).

The phosphorus levels in the soil A horizon under all trees is too low for a net mineralization to occur (Stevenson, 1986). The accumulated amounts of phosphorus under indigenous and deciduous trees are most certainly temporarily immobilised and incorporated into the soil microbial biomass.

FIGURE: 6.4.1.n

PHOSPHORUS

■ 0 - 1 cm ▨ 7 - 8 cm ☐ 14 - 15 cm

mineral P 4.6 - 5.5 mg/kg
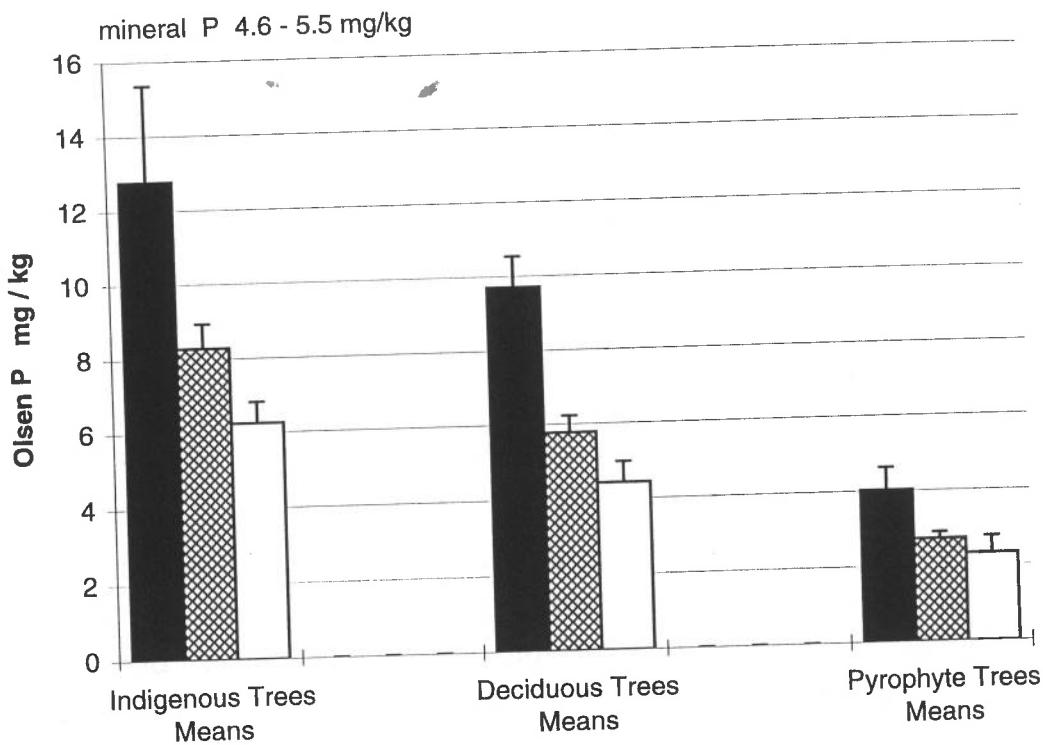
FIGURE: 6.4.2.n

Phosphorus

■ 0 - 1 cm ▨ 7 - 8 cm ☐ 14 - 15 cm
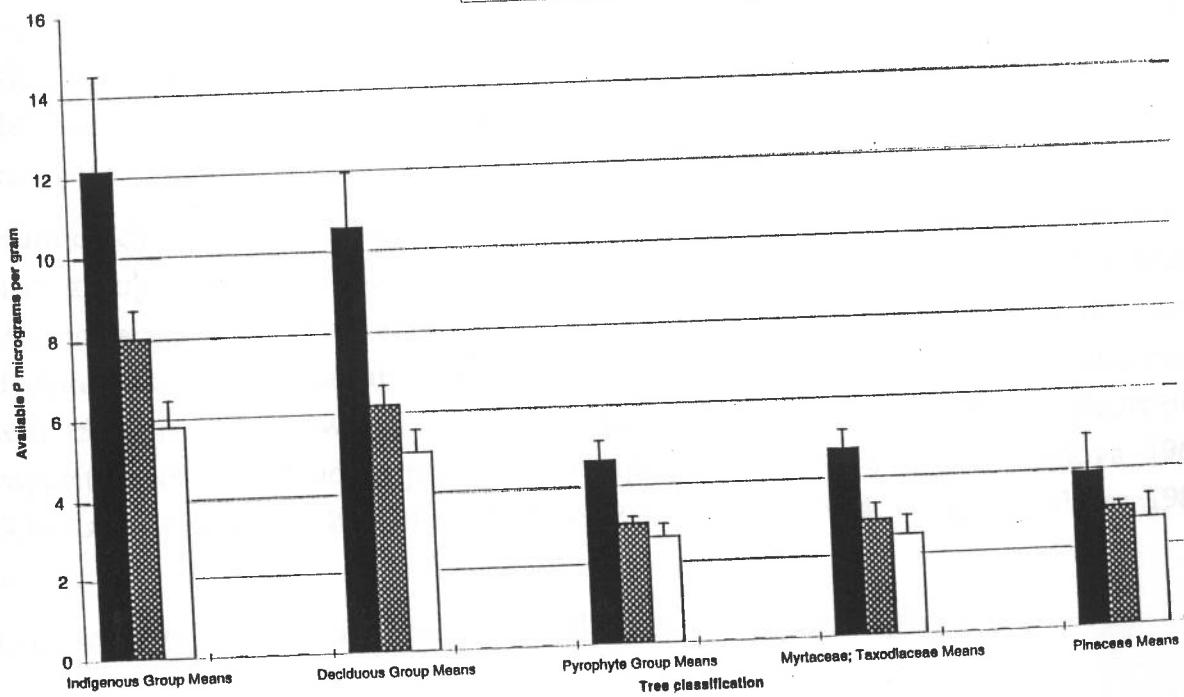
6.4.1.2.0:   Humic acid fraction (Fig. 6.4.1.o).

The differences between the tree groups are highest for the humic acid fraction and lower for the fulvic acid fraction.

The humic acid fraction differs considerably between the tree assemblages. Highest percentages are reached under the indigenous trees. The variation within the group is quite high and reflects the site variations, discussed in relation with the carbon soil parameter. Of interest are the high amounts and variations of humic acids under particularly indigenous trees and also exotic deciduous trees at the mid-soil depth of 7 - 8 cm.

The fire trees show considerably less humic acids and small standard errors, particularly at the lower soil levels. The humic acid contents decrease with increasing soil depth for all exotic gymnosperms and eucalypts (Appendix: B; Table 2).

The dendrogram based chart on **humic acid (Fig. 6.4.2.o)** shows trends of decreasing amounts with soil depth under the "pyrophanerophyte" group. However, both "indigenous" and "deciduous" groups show highest amounts of the humic acid fraction, in the middle of the A-horizon at 7-8 cm. The highest amounts are depicted for the "indigenous" group, the lowest amounts for the *Pinaceae*.

General features of humic acids are described below.

The importance of humic material compared to clay minerals for the storage and exchange of cations and anions is illustrated by its potential exchange capacity, which is estimated to range from 200 to over 500 me%. The exchange capacities of clay minerals ranges from 5 to 15 me% for Kaolinite, from 20 to 50 me% for Illite and from 80 to 150 me% for Montmorillonite and Vermiculite, (Schroeder, 1983).

Humic acids are spherocolloids with a high degree of polymerization. The active side groups include carboxyl, hydroxyl, methoxyl, carbonyl and amino groups. Humic acids represent a relatively stable product of predominantly biotic decomposition processes and, dependent on the litter quality, may form complexes with clay substances, which delimits the mobility in the soil. Both, the adsorption capacity and water holding potential are high (Scharpenseel, 1961; Kononova, 1966, Schnitzer, 1971, Swift, 1979, Stevenson, 1982, Schroeder, 1984, Koegel-Knabner, 1988, 1990).

Characteristic features of humic acids will be discussed in chapter 8.

FIGURE: 6.4.1.o

HUMIC ACID

■ 0 - 1 cm ▨ 7 - 8 cm □ 14 - 15 cm

FIGURE: 6.4.2.o

Humic Acid

■ 0 - 1 cm ▨ 7 - 8 cm □ 14 - 15 cm
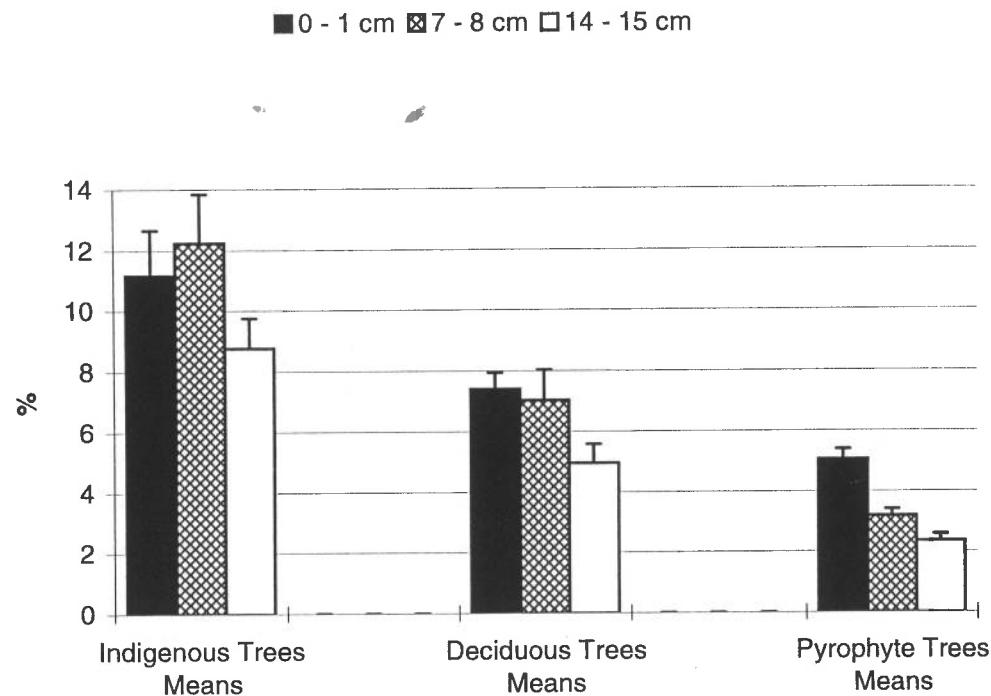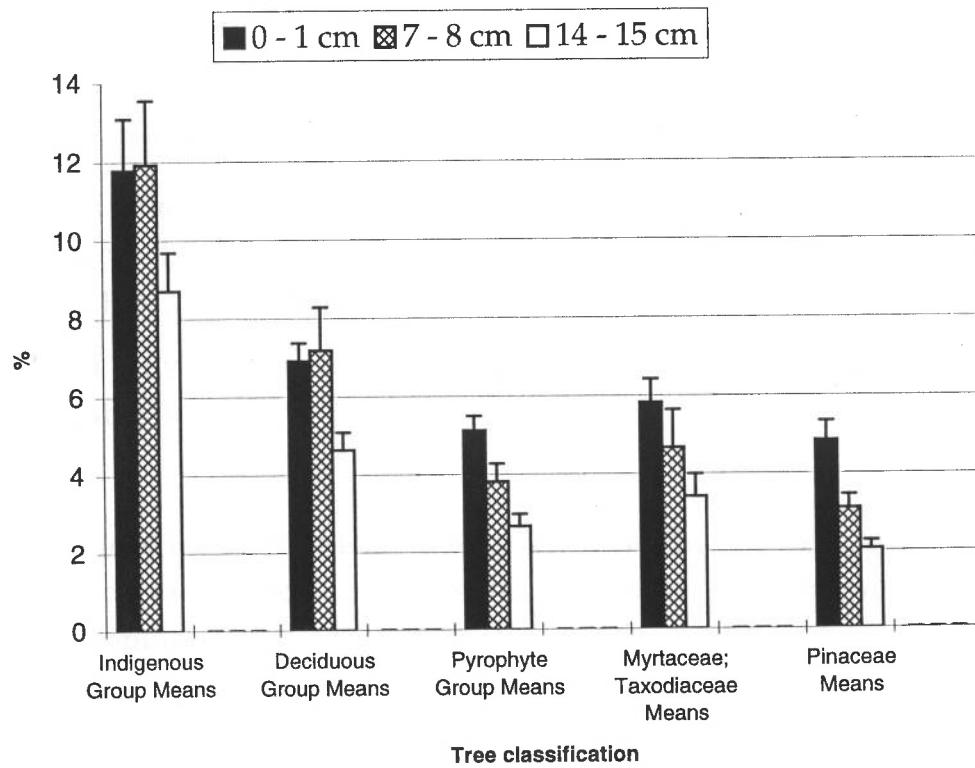
6.4.1.2.p: Fulvic acid fraction (Fig. 6.4.1.p).

The differences between tree associations and soil depths are smaller compared to other soil parameters. It is interesting to note that under indigenous trees the amounts of fulvic acids are lowest at the mid soil level and seem to be negatively correlated to highest amounts of humic acids at this level. The lowest amounts of fulvic acids are found under fire trees. The total amounts are not as different from the deciduous group as the humic acid fraction.

Similarly, under the influence of the dendrogram defined "pyrophanerophyte" group the amount of the **fulvic acid fraction** decreases with soil depth **(Fig. 6.4.2.p)**. The "deciduous" group shows smaller variations between soil depth and shows a higher mean at the lowest soil level, when compared to the mid soil level. The highest overall amounts of fulvic acid are found under the "indigenous" group. The lowest amounts are found under the *Pinaceae* at all soil depths. At the upper most soil level there are little differences between the "deciduous" group and the myrtax group. The differences however increase with soil depth, due to a reduced amount of fulvic acid under the myrtax group with soil depth.

Fulvic acids are spherocolloids with a low degree of polymerisation and a carbon/oxygen ratio of about 1 (Schnitzer, 1971).

The mobility in the soil is high. Adsorption to Si oxide of clay minerals is significant only at a pH level of < 3.5 (Schulthess, 1991).

The nutrient adsorbtion capacity and the potential to hold water is lower.

The occurrence is more pronounced in a nutrient poor soils with limited biotic activity (Scharpenseel, 1961; Kononova, 1966; Schnitzer, 1971; Swift, 1979; Stevenson, 1982; Schroeder, 1984; Koegel-Knabner, 1988; 1990).

The amounts of fulvic acid are rather variable between soil depths and trees (Appendix: B; Table 2).

The ratio of humic to fulvic acids is close to unity under the fire trees, whereas under the indigenous and exotic deciduous trees the mean ratio varies between 2 and 3 at the various soil depths.

FIGURE: 6.4.1.p

FULVIC ACID

■ 0 - 1 cm ⊠ 7 - 8 cm □ 14 - 15 cm
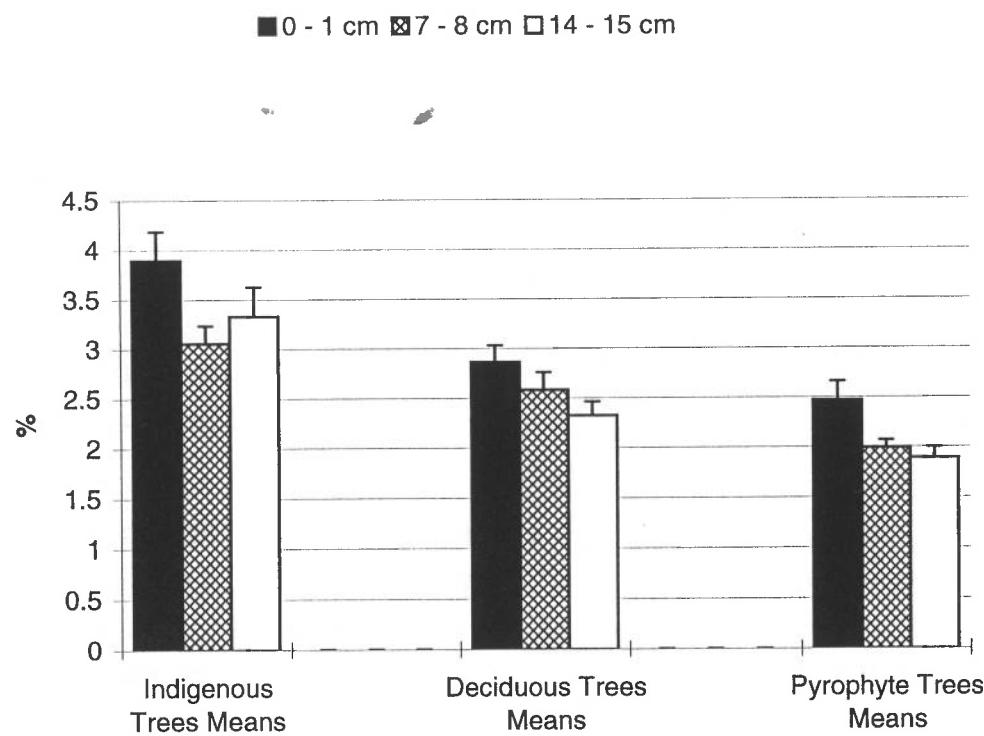
FIGURE: 6.4.2.p

Fulvic Acid

■ 0 - 1 cm ⊠ 7 - 8 cm □ 14 - 15 cm
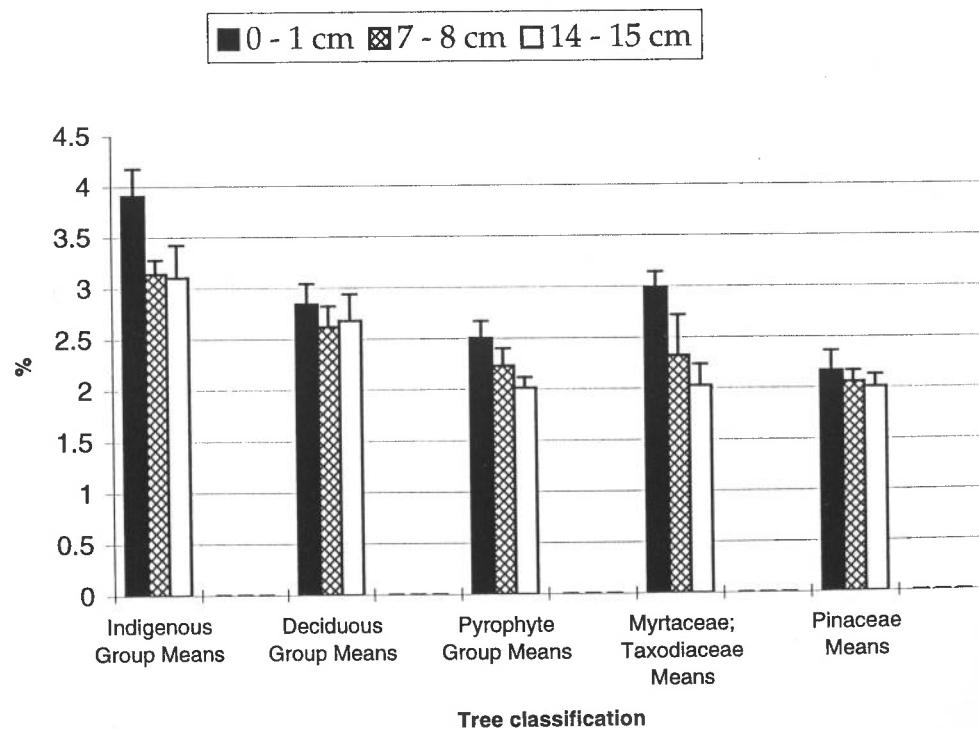
6.4.1.2q: Humin fraction (Fig. 6.4.1.q).

The humin fraction consists of the soil organic matter that remains unaffected by extracton methods and comprises various components at different soil depths and under different primary producers.

At the upper soil level the major contributors to the humin fraction consist of semi-decomposed plant material and soil biota. At the lower soil levels humins may represent soil biota and derivates of altered, "inactivated" humic substances.

Humin contents commonly decrease with soil depth. The differences at the upper soil level between tree groups are not great, but are likely to consist of different components. At the lower soil levels the *Pinaceae* show particularly low amounts of humin substances, compared to the other trees (Appendix: B; Table 2).

The composition of the **humin fraction (Fig. 6.4.2.q)** differs considerably between the dendrogram groups. Highest amounts are again found under the "indigenous" group, followed at the lower soil levels by the "deciduous" group. The myrtax group shows high amounts of humin in the upper soil horizon, and the large difference between the humin amounts in the upper soil horizon and the lower horizons is typical of a mor humus development under both the myrtax group and the *Pinaceae*.

The common characteristics of humin substances include high molecular carbon contents of >60 %, a weak acidity and a high degree of polymerisation. The adsorption capacity is smaller, compared to humic acids (Scharpenseel, 1961; Kononova, 1966, Schnitzer, 1971, Swift, 1979, Stevenson, 1982, Schroeder, 1984, Koegel-Knabner, 1988, 1990).

FIGURE: 6.4.1.q

Humin; Biomass
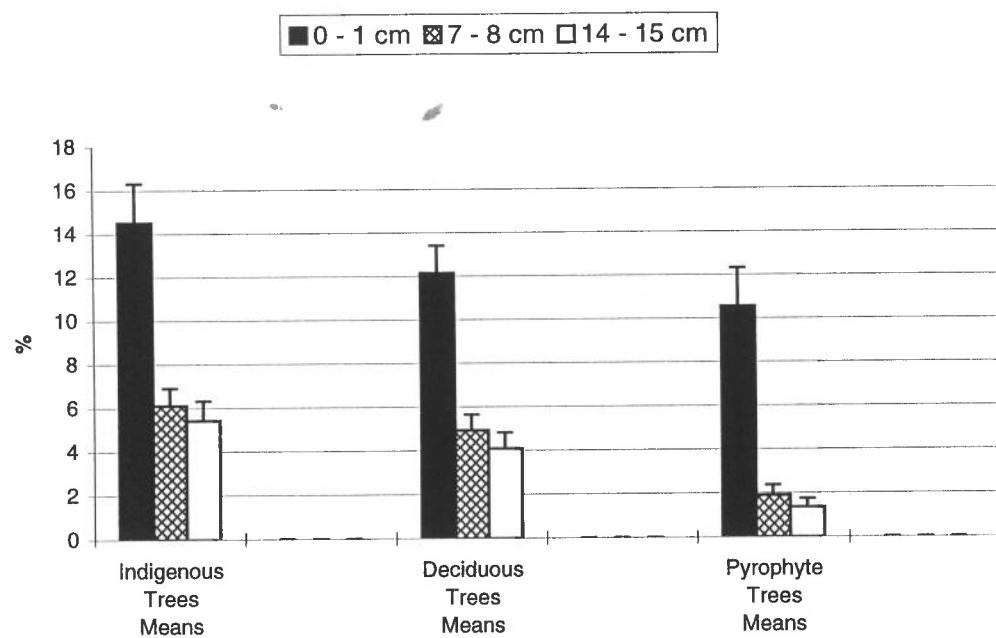
FIGURE: 6.4.2.q

Humin
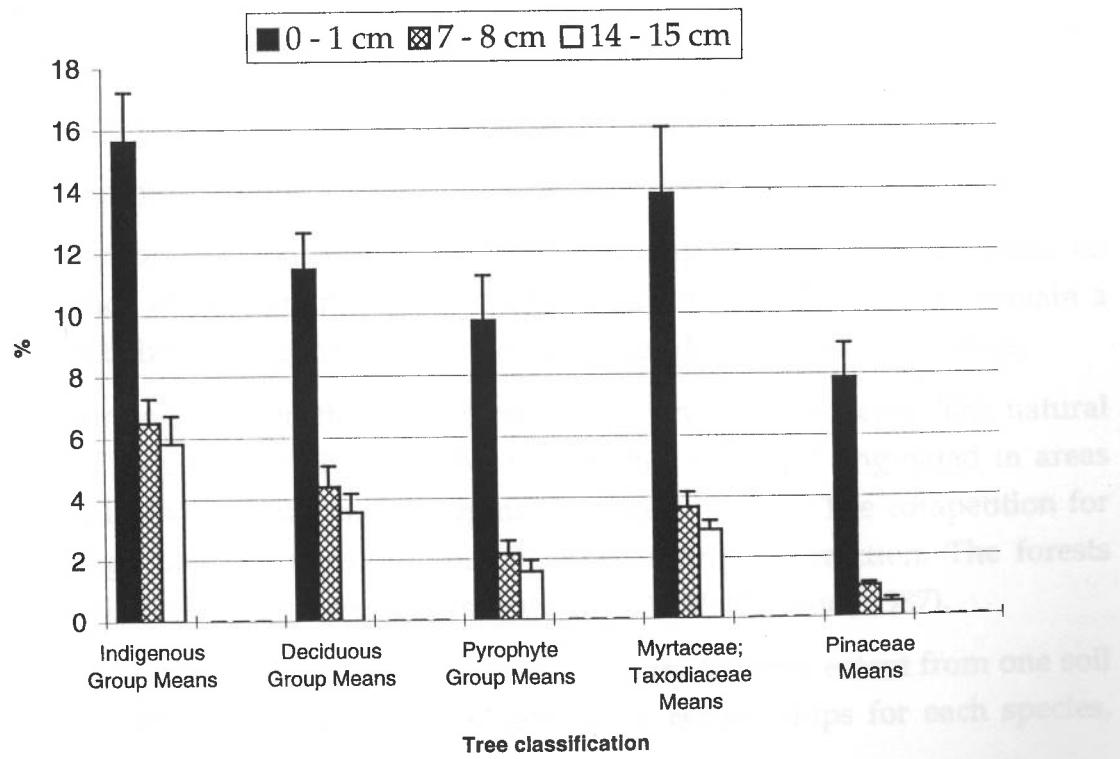
6.0.0.2.   Synopsis.

The two tree classifications, based on the P.C.A. and on the cluster analysis sorted the trees according to their influence on the soil. Both classifications demonstrate that similar nutrient cycling strategies are used by phylogenetically different trees and trees of different origin, which have evolved independently but under similar environmental conditions.

The cluster analysis for the combined soil depths was used to regroup all species exclusively on the relationship of soil parameters, irrespective of the origin of species.

Site homogeneiety.

In addition to the data of Tomlinson, Leslie (1977) and the subsoil pH measurements, the dendrograms of the cluster analysis confirm that there is no noticeable difference in the mineral composition between the sites. At the soil depth of 14 - 15 cm the trees do not indicate any site-specific clustering. *Nothofagus truncata* is associated with *Fraxinus excelsior* at the lowest soil depth level. Positions of *Kunzea ericoides* with *Cryptomeria japonica* and *Pseudotsuga menziesii* and *Eucalyptus regnans* with soil depths demonstrate that differences are caused by the flora, rather than the sites. The Mt. Cargill site was thought to have the potential to be different due to phonolite in the sub-soil loess matrix. The position of *Dacrydium cupressinum*, relative to *Prumnopitys ferrugineus* and *P. taxifolia* and the latter two to *Nothofagus fusca* and *Nothofagus truncata* demonstrates that there is no significant site difference in the mineral composition of the soil A-horizon and that the influence of the unmodified forest is the determinant of the position of trees relative to one another.

"Pyrophanerophyte" group.

All pyrophanerophytes identified by the principal component analysis are found on one main branch of the dendrogram throughout all soil depth levels and remain a distinct group to both, indigenous trees and exotic deciduous angiosperm trees.

This distinction is based on the adaptation to different environments. The natural distribution of pyrophanerophyte species is restricted to -, and originated in areas that are edaphically or climatically marginal for forest growth. The competition for nutrients is high and the trees are specialized in nutrient extraction. The forests typically contain little tree species diversity (Walter, 1987; Delcourt, 1987).

The groupings and relationships of the other trees vary to some extent from one soil depth strata to the other and reflect soil parameter relationships for each species,

which were outlined in the description of the ordinations based on the principal component analysis (section 6.1).

"Indigenous" group and "Deciduous" group.

The upper soil strata dendrogram demonstrates differences between, on one side an assemblage of some indigenous emergent and canopy species (*Prumnopitys* spp. and *Nothofagus fusca* and *N. truncata*) and on the other side, all other indigenous and exotic deciduous trees.

This indicates that there is a distinction in the direction of nutrient cycling within the indigenous forest ecosystem between subcanopy species and canopy species.

The canopy and emergent species of this study produce litter that encourages the formation of large amounts of humic material, which leads to a substantial increase of the C.E.C.. *Fuchsia excorticata*, *Sophora microphylla* seem to cycle phosphorus efficiently (see Appendix: B; 2) and other subcanopy species might be best equipped for the cycling of other nutrients (refer to 8.3.1. and Enright and Ogden, 1987).

Both, indigenous and deciduous sub-groups have predominantly exotic deciduous trees at their respective centres in the soil strata dendrograms.

The three exotic deciduous species, *Acer pseudoplatanus*, *Ulmus procera* and *Tilia europaea*, form a permanent core within the "indigenous" group, which is composed of a further six permanent species, namely *Prumnopitys ferruginea*, *P. taxifolia*, *Nothofagus fusca*, *N. solandri*, *N. truncata* and *Plagianthus regius*. Another two exotic deciduous angiosperms join the "indigenous" group at various soil depth levels. *Aesculus hippocastaneum* can be found in association with the "indigenous" group at the upper soil level and *Fraxinus excelsior* joins the "indigenous" group at the lowest soil depth strata.

The "deciduous" group includes *Acacia melanoxylon* and *Cryptomeria japonica* at the upper soil strata and a further four indigenous trees *Dacrydium cupressinum*, *Fuchsia excorticata*, *Kunzea ericoides* and *Sophora microphylla*, whose position within the deciduous group is dependent on soil depth.

Convergences in the cycling of nutrients.

It is interesting to note that both, the "indigenous" group and the "deciduous" group are composed of a core of mull humus type forming trees, which are associated with tree species, whose litter is known to encourage the formation of the moder humus type.

The mull humus type in the "indigenous" group is formed by the genera *Ulmus, Tilia, Acer,* (C/N 16-22 across the soil profile) *Plagianthus, Prumnopitys ferruginea* and *Sophora* (C/N 12-32). The associated plants that encourage the formation of the moder humus type belong to the genus *Nothofagus* and *Prumnopitys taxifolia,* with a C/N ratio ranging from 33 to 49 at the upper soil horizon and decreasing with soil depth to a C/N ratio of 16 to 32.

The formation of the mull humus type in the "deciduous" group is encouraged by the genera *Fraxinus, Ulmus, Aesculus,*(C/N 11-23) *Fuchsia* (C/N 17-31). The other genera have been reported to shed litter with moder humus type forming qualities (Dengler, 1992, Walter, 1987, Roehrig, 1991). The C/N ratios of the genera *Quercus, Fagus* and *Dacrydium* range between 13 and 23, which is in the traditional range of the mull humus type. This ratio might have been influenced by litter additions of adjacent indigenous subcanopy species, such as *Melicytus ramiflorus.*

The main soil parameters responsible for the division of the "indigenous" and the "deciduous" groups seem to be mainly the C.E.C. and the exchangeable bases.

While the base saturation of both groups is rather similar, the C.E.C. and the exchangeable bases are significantly higher in the "indigenous" group and specifically under *Tilia europaea, Ulmus procera, Acer pseudoplatanus, Plagianthus regius* and the species of *Nothofagus.*

Various convergent nutrient cycling strategies of individual trees, which were indicated by the P.C.A. ordination are confirmed by the cluster analysis.

Additional subtle convergent strategies are indicated between various phylogenetically distinct members of the indigenous forests.

A clustering of indigenous canopy and emergent trees is evident at the upper soil horizon. These canopy trees are the gymnosperms *Prumnopitys ferruginea* and *P. taxifolia* and the angiosperms *Nothofagus fusca,* and *N. truncata.* The clustering could be associated with the initial resistance to decomposition (waxed leaf surface, lignins, phenols) of an otherwise nutrient rich litter (see Appendix: B; Table 2), leading to a soil surface moder humus type.

The assumption that canopy species and subcanopy species from both, northern and southern Hemisphere temperate forest biomes evolved similar nutrient cycling strategies becomes apparent in the following examples.

The genera *Dacrydium* and *Cryptomeria, Prumnopitys, Nothofagus* and *Fagus* shed litter that initially resists decomposition and, in combination with moderate amounts of

exchangeable bases, leads to the formation of a moder type humus. All are species of the forest canopy.

Acer pseudoplatanus displays a close relationship at the upper soil level with *Nothofagus solandri* and at the lower soil levels with *Nothofagus fusca* with regard to the individual nutrient cycling strategies.

Similarly, *Quercus robur* and *Acacia melanoxylon* demonstrate convergent nutrient cycling strategies throughout the soil profile.

Another obvious convergence involves *Plagianthus regius, Ulmus procera* and *Tilia europaea.*(Figs. 6.2)

Tilia europaea and *Nothofagus truncata* show convergences below the soil surface, within the soil A-horizon.

These examples show that the nutrient cycling strategies of both groups are closely related, and part of two distinct and coherent forest ecosystems, which have evolved separately, under similar environmental conditions and with similar ecosystem-evolutionary objectives with regard to the storage of nutrients in the soil.

The various positions on the dendrogams, of indigenous and exotic deciduous species with soil depths and from one tree group to the other, indicate that individual nutrient cycling strategies cover a broad spectrum.

Individual nutrient cycling and - storage strategies combine to secure long-term advantages for the procreation of the entire forest ecosystem, by minimizing the loss of stored energy and nutrients from the system, increasing the nutrient storage and - cycling capacity and providing inertia against environmental perturbations.

6.0.0.3. Discussion

Tomlinson and Leslie (1977) suggested that the clearance of the indigenous vegetation was followed by decades of soil erosion. The common soil A-horizon depth of < 20 cm at the four survey sites (Flagstaff; Opoho; Orokonui; Town Belt) supports this suggestion, if it is compared with > 25 cm of soil A-horizon of the unlogged and steeper Mt. Cargill site. However, despite the post clearance erosion-loss of perhaps more than one fifth of the soil A-horizon, it can be assumed that the soil parameters of the A-horizon were higher than the mineral contribution, due to the likely presence of indigenous nutrient stores in the form of humic matter at the time of re-planting.

The supposition of mineral homogeneity made it reasonable to assume that the substantial differences of nutrient content in the soil A-horizon are caused by specific autotrophic litter input and associated divergent soil biotic activities, resulting in substantial variations of organic cation exchange sites on humic molecules, and affecting the storage capacity of the soil, as well as the physical soil structure.

Common to all tree groups is the general decrease of nutrients with soil depth.

The total soil-nutrient amounts however vary significantly between tree groups.

The indigenous group shows highest values for some soil parameters, such as organic matter, carbon, humic acid, fulvic acid, phosphorus, which to some degree is associated with the inclusion of the three indigenous gymnosperms from the undisturbed Mt. Cargill site, where nutrient loss through biomass removal never occurred.

The results for all soil parameters under both, indigenous and exotic deciduous groups are indicative of effective nutrient cycling strategies and nutrient storage increases in the mineral soil, as implied by the substantial stepped increases of most soil parameters towards the top of the organic-mineral soil horizon. Notable exceptions to this trend include the parameters Mg and Na.

The nutrient contents of the soil A-horizon are far lower under Pinaceae and eucalypts, when compared to the other tree groups. Most soil parameters at all depths of the soil A-horizon are below -, or within the range of the nutrient contents of the common mineral loess substrate.

There is no indication, that pyrophanerophytes effectively cycle and incorporate nutrients into the mineral soil. Under the consideration of the likely presence of indigenous nutrient stores at the time of planting, these values are indicative of the

dominance of nutrient extraction processes, over processes that lead to increases of soil nutrient storage.

The generally harsh environmental conditions (extremes of temperature, pH; soil water deficits) of the natural habitats of pyrophanerophytes are not conducive to increases of soil nutrient storage (Walter, 1987; Appendix: A; 2), and provide an explanation for the biological adaptations of pyrophanerophytes in producing litter, that does not lead to an increase of soil nutrient storage and that could not support a process of nutrient cycling via an organo - mineral soil complex.

Biological adaptations to such environmental conditions necessitate the evolution of effective methods for the extraction of mineral nutrients (Pryor, 1976; Marschner, 1986; Walter, 1987; Leyval, 1990).

Significantly decreased pH values are associated with increases of mineral wheathering, (Jenny, 1980; Schröder, 1983; Stevenson, 1986) which are characteristic for a prevalence of nutrient extraction strategies (Ulrich, 1987; Roehrig, 1991).

These are characterized by:

1) the accelerated weathering of minerals, via root exudates and litter-leachates of organic acids, and

2) the decomposition of organic nutrient stores, via mycorrhizal associations.

1) "The release of relatively large amounts of organic acids is a typical feature of plant species, adapted to highly acid mineral soils" (Marschner, 1986).

The efficiency with which a root system mobilizes mineral nutrients in the rhizosphere via,

1.1) acidification (net release of H^+ ; the excretion of HCO^{3-} and the evolution of CO_2 by respiration) and via

1.2) variable amounts and compositions of root exudates (organic acids, sugars, amino acids, phenolic compounds)

is species specific (Marschner, Roemheld, 1983), partly a function of the local rooting density and the nutrient availability of the substrate (Marschner, 1986).

Enhanced "weathering" of soil material is indicated by the accumulation of amorphous iron and aluminium oxyhydrates, following the disaggregation of polymineralytic shale particles at the soil-root interface, particularly in soils, low in available potassium (Sarkar, et al., 1979).

The accumulation of nutrient ions in the rhizosphere is closely related to the transpiration rate, which typically remains high for many eucalypts, even when under water stress (Pryor, 1976). The complexation of aluminium by polyphenols or organic acids, leached from leaves or litter might offer an indirect way for certain *Eucalyptus* spp. to achieve both, high aluminium tolerance and acquisition of phosphorus from extremely deficient soils (Ellis, 1971).

Kononova (1966) suggested that under certain environmental (temperatures of the boreal zone) or biological conditions (coniferous litter), humic acids are fulvic acid like, highly mobile and leachable, thereby assisting in the weathering of minerals.

2) Research by Toutain (1981) suggests that actinomycetes and filamentous fungi are responsible for the decomposition of humic polymeric nuclei, which suggests that ectomycorrhizae of firetrees might decompose and feed on the organic nutrient stores, that were left by the previous vegetation and use the humic material as a source of N.

The weathering of minerals and the decomposition of organic nutrient stores results in rapid "soil ageing" (Jenny, 1980), the formation of an Ae -horizon and the soil degeneration to a podzol (Ulrich, 1987).

These nutrient extraction strategies explain the growth rates of firetrees, planted on previous forest-soil systems, that were based on nutrient cycling and storage.

In chapter 8 these dynamics will be discussed in greater detail.

6.5.0.0   ANOVA derived HYPOTHESES

The analysis of variance has rejected both null hypotheses,

H_O 1:"The influence on the soil of all examined trees is the same."

H_O 2: "There is no difference between the tree groupings in the soil parameters, the the amounts of the humic fractions and their particular ratios."

The following alternative hypotheses were accepted on the basis of the results of the analyses of variance of the P.C.A. tree groups, which were supported by the ANOVA of the dendrogram derived tree-groups.

H_A 1)   Specific tree influences on soil develpoment are shown by significant differences between tree groups for soil parameters and are indicated by the spread of individual indigenous and deciduous tree species within the ordinations.

H_A 2) The differences for humic acids are significant at all soil depth levels between the indigenous -, the exotic deciduous trees and the pyrophanerophytes.

The fulvic acid fraction has significant differences confirmed between indigenous trees and pyrophanerophytes at all soil depth levels,

and between the exotic deciduous angiosperms and the pyrophanerophytes at the mid soil depth level and the indigenous and exotic deciduous angiosperm group at the lowest soil depth.

H_A 3A)   Pyrophanerophytes display nutrient extraction strategies, which are significantly different to

H_A 3B)   the nutrient cycling strategies that are demonstrated by the indigenous angiosperms and - gymnosperms and the exotic deciduous angiosperms.

Considering the natural longevity of humic substances (Stevenson, 1982; Swift, et al., 1979, 87), the presence of indigenous nutrient stores in the form of humic-mineral complexations can safely be assumed at the time of pyrophanerophyte establishment.

Nutrient extraction associated with the decomposition of indigenous humic mineral complexations are indicated by the mineral nutrient contents of the soil A-horizon, that do not significantly exceed those of the mineral substrate.

Significant differences between pyrophanerophytes and other tree groups have been shown for all soil parameters and at all soil depth levels (with a level of confidence of 95 %; $p = < 0.05$).

Nutrient cycling is indicated by significant soil parameter increases of the soil A-horizon over those of the mineral substrate.

H_A 4) No significant differences between the indigenous trees and the exotic deciduous angiosperms were attained for most soil parameters and at most soil depth levels.

Significant differences between the indigenous trees and the exotic deciduous angiosperms were obtained for the amounts of carbon and humic acid at all depth levels, fulvic acid at the lowest soil depth and phosphorus at the two lower soil depth levels and were possibly site related (inclusion of three trees from the undisturbed Mt. Cargill site).

The analyses of variance based on the dendrogram tree groups confirmed the hypotheses H_A 1; 2; 3 , that were generated from the first, P.C.A. based ANOVA.

The differences between the "pyrophanerophyte" group and both "indigenous" and "deciduous" groups for all soil parameters remained significant at almost all soil depth levels.

There were some soil parameter differences between the component groups of the "pyrophanerophyte" group, the *Pinaceae* and the myrtax group.

The *Pinaceae* and the myrtax group show significant differences for the following soil parameters and

...at all soil depth levels: magnesium; organic matter; humin.

...at the upper soil level: sodium; fulvic acid; nitrogen; humic acid nitrogen.

...at the mid and/or lower soil depth level: field to air dry soil moisture; base saturation; total exchangeable bases; potassium; sodium; humic acid; carbon; ratio humic acid/fulvic acid.

The nutrient extraction strategies of pyrophanerophytes cover a limited range of responses, primarily related to differences in the amounts of hydrophilic and leachable organic fractions produced and the different preferences of internal versus external cycling of magnesium.

The majority of soil parameters shows no differences between the Pinaceae and the myrtax group. And considering the tight distribution of the *Pinaceae* and the *Myrtaceae*, specifically *Eucalyptus regnans*, on the P.C.A. ordination the following alternate hypothesis can be formulated:

H_A 5) Trees of distant phylogenetic and ecological origin can have convergent nutrient cycling strategies.

Subtle convergent strategies are also indicated between various members of the indigenous forests and the exotic deciduous forests. The data presents indications, that convergences with regard to nutrient cycling strategies exist within the vertical stratifications of both, indigenous and deciduous biomes, for example canopy species and subcanopy species (see 6.0.0.2; 6.0.0.3). The tree grouping based on the dendrogram ordination shows associations of indigenous and deciduous trees that are based on the quantitative similarity of nutrient cycling (C.E.C.; T.E.B.), while combining species with various qualitative effects on the soil (C/N ratio).

These will be investigated in more detail with the correlation of soil parameters in section 6.6. and additional hypotheses will be confirmed in section 6.7.

6.6.0.0   Correlations of soil parameters between and within tree groups.

Introduction

Correlations of soil parameters were used to examine between and within tree group variation, to help clearify the factors involved that led to the ordination of species and to elucidate specific strategies operating within a forest ecosystem.

Significant correlations between soil parameters will examine H_A 1; 3 and 5 and test further hypotheses.

All correlations mentioned in the text are significant at ($p = \, < 0.05$), unless otherwise stated.

Obvious correlations, like Ca with B.S. or T.E.B. are not specifically mentioned in the text. Neither are correlations, where the range of values was deemed responsible, rather than the effect of trees or tree groups.

The figures 6.6.2a and tables (Appendix: B; 4) illustrate the positive or negative correlations of various soil parameters at the three soil depths.

The correlations on the P.C.A. deciduous tree group show that the soil parameters C.E.C. and T.E.B. are dependent variables. The tree groups were subjected to a regression analysis at each soil depth level for both parameters to produce graphs that depict the variation between groups. The regression analysis on the dendrogram groups underlines the importance of both parameters in the definition of the tree grouping.

6.6.0.1 Methods

Soil parameters were log transformed where necessary thus enabling the correlation of soil parameters and measuring the relationship of various data sets that are scaled to be independent of the unit of measure.

The correlation coefficient, r, for $p = 0.05$ was 0.632 for the indigenous and the deciduous groups, which had 10 replicates each. The pyrophanerophytes of the P.C.A. ordination consisted of eight replicate trees, whereas the "pyrophanerophyte" group consists of 10 replicates. The critical value of r ($p = 0.05$) for the former amounts to 0.707. The sub-groups of the "pyrophanerophyte" group, the myrtax group and the Pinaceae consisted of five replicate trees each, with a critical value r ($p = 0.05$) of 0.878 . Brackets around soil parameters on tables 6.6 denote correlation

coefficients at (p=< 0.1). The referred to correlations are significant (p = < 0.05) unless otherwise stated.

Tree groups of both classifications, P.C.A. ordination and Cluster analysis, were subjected to a regression analysis for the soil parameters C.E.C. and T.E.B., at the three soil depths. The linear regression describes Y as a function of X within the range of observed values of X. The general equation used for the straight line of the simple linear regression is $Y_i = \alpha + \beta X_i$. The results are depicted as Figures 6.6.1 a-c and 6.6.2 a-c.

6.6.0.2 Results

6.6.1.2.   Significant correlations of soil parameters;

comparison between P.C.A. tree groups.

Tables 6.6.1 a - c demonstrate the significant correlations (p = < 0.05) between soil parameters for each of the three soil sections, brackets denote correlations that are significant at (p = < 0.1).

The most striking differences between the three P.C.A. derived phanerophyte associations relates to correlations between C.E.C. and T.E.B..

Under the exotic deciduous angiosperm trees there is a significant positive correlation (p < 0.05) between the C.E.C. and the T.E.B. at all soil depth levels.

The correlation is insignificantly positive under the indigenous trees, at levels of significance between 80 % (p=< 0.2) at the lowest soil level, rising to 90 % (p= < 0.1) at the upper soil level.

Under pyrophanerophytes however, there is no correlation between C.E.C. and T.E.B. at all soil depth levels. (see section 6.6.1.3)

The C.E.C. under indigenous and exotic deciduous trees is generally positively correlated to soil organic matter, (decid. at 0-1cm 94%; p = < 0.1) soil carbon and soil moisture (indig. at 0-1cm 83%; p = < 0.2) at all soil depth levels.

Positive correlations of C.E.C. with humic acid are significant under the indigenous trees at the upper and mid soil level and under the exotic deciduous trees at the lowest soil depth level.

Under fire trees, the C.E.C. has few correlations with other soil parameters. There is a positive correlation with soil organic matter at the upper most soil level and a positive correlation with the humic acid fraction at the lowest soil level caused by the *Myrtaceae*.

Under indigenous and exotic deciduous trees, a positive correlation exists for C.E.C. and nitrogen at the lower two soil levels.

C.E.C. and the humic acid fraction are positively correlated under both vegetation types at the lower two soil levels.

Under exotic deciduous trees 93% (p = < 0.1) are reached for positive correlations between C.E.C. and both, the humic fraction and base saturation, at the lowest soil level.

The correlations for the **humic acid fraction** are significant with carbon, at the <u>upper soil level</u> under all tree groups, under deciduous trees carbon and soil organic matter correlations reach 93 % (p = < 0.1). The indigenous trees show additional positive correlations with C.E.C., nitrogen, fulvic acid and sodium.

At the <u>mid soil levels</u> positive correlations of humic acids exist with nitrogen under both indigenous and exotic deciduous angiosperms.

Fire trees however show negative but insignificant (- 87%; p = < 0.15) correlations between humic acid and nitrogen.

Under the exotic deciduous angiosperms and at the <u>lowest soil level</u> the correlations of humic acid are positive with the exchangeable bases T.E.B., calcium and the cation exchange capacity C.E.C..

Under the indigenous trees humic acids are positively correlated with fulvic acids, carbon and soil organic matter.

Under the fire trees a positive correlation of humic acids with C.E.C. exists at the lowest soil level.

The **fulvic acid fraction** under indigenous trees is positively correlated with soil organic matter, humic acid, carbon, nitrogen and sodium at the <u>upper most soil level</u>.

Under the influence of exotic deciduous trees, insignificant positive correlations exist with the T.E.B. and nitrogen (at 88 %; p = < 0.15) at the upper soil level.

The fire trees show positive correlations between fulvic acids and nitrogen and insignificant positive correlations with soil organic matter at 92% (p = < 0.1).

At the <u>mid soil level</u> the fulvic acid fraction under indigenous trees is positively correlated (p = < 0.05) with potassium, sodium, soil moisture, nitrogen and C.E.C..

Under deciduous trees there are no significant correlations at this soil level with the fulvic acid fraction.

Under fire trees positive correlations are shown with phosphorus at the mid soil level.

The <u>lowest soil level</u> shows positive correlations (p = < 0.05) between fulvic acids and soil organic matter, carbon and humic acid under indigenous trees.

CORRELATION CONFIDENCE 95%	pos/neg.	Indigenous trees 0-1 cm	Deciduous trees 0-1 cm	Pyro-phanerophytes 0-1 cm	Myrtaceae 0-1 cm	Pinaceae 0-1 cm
Moisture content air to oven dry {ODM}	positive			(HA)	TEB.HA	
	negative					
pH	positive	BS.;Ca.;TEB.;(P)	BS.;Ca.;K.;TEB	BS.;Ca.;K.;TEB.;P	BS.;P	BS.;TEB.;Ca.;Mg.;K.;P
	negative	pH.;Ca.;TEB.	pH.;Ca.;K.;TEB	pH.;Ca.;(Mg);K.;TEB.;P.	pH.	pH.;TEB.;Ca.;Mg.;K.;
Base Saturation {BS}	positive	pH.;BS.;Ca.	pH.;ODM.;BS.,CEC.;Ca.;K.	pH.;BS.;Ca.;Mg.;K.;P.	ODM.;Ca.	pH.;BS.;Ca.;Mg.;
	negative	Mg.	Mg.			
Total exchangeable Bases {TEB}	positive	pH.;BS.;TEB.	pH.;ODM.;BS.,CEC.;K.;TEB	pH.;(BS.;Mg).;K.;TEB.;P.	TEB.	pH.;BS.;TEB.;Mg
	negative	Mg.	Mg.			
Ca	positive	CEC.;Ca.;TEB.	CEC.;Ca.;K.;TEB.			pH.;BS.;TEB.;Ca.;K
	negative		pH.;BS.;Ca.;TEB			
Mg	positive		Mg.	(BS.;Ca.;N).;K.;TEB.		
	negative				(K.;N)	
K	positive			pH.;BS.;Ca.;Mg.;TEB.;P.		pH.;BS.;Mg
	negative				(Mg)	
Na	positive	HA.;FA.		N		
	negative					
Cation Exchange Capacity {CEC}	positive	SOM.;C.;HA.	ODM.;Ca.;TEB.;(SOM.).;C	SOM.		Humin
	negative	Mg	Mg.			
P	positive	(pH).		pH.;BS.;Ca.;K.;TEB.	pH	pH.;
	negative					
Soil Organic Matter {SOM}	positive	CEC.;C.;N.;HA.;FA.	(CEC.);ODM.;C.;(HA).	CEC.;C.;N.;(FA)	FA.;Humin	HA.;Humin;C
	negative		(SOM.;C)		(K)	
Humic Acid {HA}	positive	CEC.;Na.;SOM.;C.;N.;FA.		C	ODM.	SOM.;C
	negative					
Fulvic Acid {FA}	positive	Na.;SOM.;C.;N.;HA.		(SOM).;N.	SOM.;Humin;C	
	negative					
Humin	positive				SOM.;FA	CEC.;SOM.
	negative				FA	
C	positive	CEC.;SOM.;N.;HA.;FA.	ODM.;CEC.;SOM.;(HA).	SOM.;HA.	FA	SOM.;HA.;Humin
	negative		ODM.			
N	positive	SOM.;C.;HA.;FA.		Na.;SOM.;FA.;(Mg).	(Mg)	
	negative					

TABLE: 6.6.1 a

Correlation (p = < 0.05) of Soil parameters

Principal Component Analysis Tree Groups

CORRELATION	pos/neg.	Indigenous trees 7-8 cm	Deciduous trees 7-8 cm	Pyro-phanerophytes 7-8 cm	Myrtaceae 7-8 cm	Pinaceae 7-8 cm
CONFIDENCE 95%						
Moisture content air to oven dry {ODM}	positive	CEC.	CEC.;Ca.;TEB.;SOM.;C.;N.;(NA).		CEC.;P.;N	Na.;C
	negative					BS.;Ca
pH	positive	BS.;Ca.;TEB.;	BS.;Ca.;Na.(TEB).	BS.;Ca.;K.;TEB.;(Mg)		Na
	negative	pH.;Ca.;TEB.	pH.;Ca.;K.;TEB.	pH.;M.;Mg.;K.;TEB.;(Na.,Ca).	Na	TEB.;Ca.;Mg
Base Saturation {BS}	positive					ODM.;C
	negative	pH.;BS.;Ca.	ODM.;BS.;CEC.;Ca.;K.;Na.	pH.;BS.;Ca.;Mg.;K.	Humin;C	BS.;Ca.;Mg.
Total exchangeable Bases {TEB}	negative					BS.;TEB.;Mg
	positive	pH.;BS.;TEB.	ODM.;BS.;CEC.;K.;Na.;TEB.	pH.;TEB.;(BS)	M.;SOM.;HA.;(Humin);C.;N	ODM.;C
Ca	negative			M.;BS.;K.;Na.;TEB.;SOM.;C.;(pH).		BS.;TEB.;Ca.;
	positive			P	CEC.;(HA)	C
Mg	positive			pH.;BS.;Mg.;TEB.		
K	positive	FA.	BS.;Ca.;TEB.		FA	ODM.
	negative				BS	
Na	positive	CEC.;(C.;N)	pH.;Ca.;TEB.;(ODM.;CEC.;SOM.;N)	Mg.;SOM.;C.;(BS).	BS	pH
Cation Exchange Capacity {CEC}	positive	ODM.;Na.;SOM.;C.;N.;HA.;(FA).	ODM.;Ca.;Na.;TEB.;SOM.;C.;N.		ODM.;P.;SOM.;HA.;C.;N	
	negative				Mg	
P	positive				ODM.;CEC.;SOM.;(HA.);C.;N	
	negative			Mg.;(M).		
Soil Organic Matter {SOM}	positive	CEC.;C.;N.;HA.	ODM.;CEC.;C.;N.	Mg.;Na.;C.	M.;Ca.;CEC.;PHA.;C.;N	HA.
	negative	CEC.;SOM.;C.;N.	N		M.;Ca.;CEC.;(P).;SOM.;C.;N	N
Humic Acid {HA}	positive					SOM.
	negative				(Mg)	N
Fulvic Acid {FA}	positive	ODM.;K.;Na.;(N.;CEC).		N	K	
Humin	positive				TEB.;(Ca).;	
C	positive	CEC.;SOM.;N.;HA.	ODM.;CEC.;SOM.;N.	Mg.;Na.;SOM.	M.;Ca.;CEC.;P.;SOM.;HA.;N	ODM.
	negative					BS.;Ca.;Mg
N	positive	CEC.;SOM.;C.;HA.;(FA).	ODM.;CEC.;SOM.;C.;HA.;(Na).	FA.	M.;ODM.;Ca.;CEC.;P.;SOM.;HA.;C	SOM.;HA
Moisture content field to air dry {M}	positive			BS.;Mg.	Ca.;SOM.;HA.;C.;N	
	negative			(P)		

Correlation ($p = < 0.05$) of Soil parameters

TABLE: 6.6.1 b

Principal Component Analysis Tree Groups

CORRELATION CONFIDENCE 95%	pos./neg.	Indigenous trees 14-15cm	Deciduous trees 14-15cm	Pyro-phanerophytes 14-15cm	Myrtaceae 14-15cm	Pinaceae 14-15cm
Moisture content air to oven dry (ODM)	positive	CEC.;SOM.;N.;(C).	CEC.;Ca.;SOM.;C.;(HA).	Ca.;Mg.;K.;(TEB.;BS).	P.;HA.;FA.;N	BS.;TEB.;Ca.;Mg.;K.
	negative			Ca.		Mg
pH	positive	BS.;Ca.;TEB.	BS.;Ca.;K.;TEB.;(SOM).	Mg.;Na.;TEB.;(Ca.;pH.;K).	K.;Humin	SOM.
	negative			(ODM)	TEB.;Na.	TEB.;Ca.;Mg.;K
Base Saturation (BS)	positive	pH.;Ca.;TEB.;(P).	pH.;Ca.;TEB.;(K).	BS.;Mg.;K.;Na.;(Ca).	BS.;Na	ODM.;C
	negative			(ODM).		BS.;Ca.;Mg.;K
Total exchangeable Bases (TEB)	positive	pH.;BS.;Ca.	pH.;BS.;CEC.;Ca.;HA.	pH.;(BS.;TEB).		ODM.;C
	negative			ODM.		BS.;TEB.;Mg.;K
Ca	positive	pH.;BS.;TEB.	pH.;ODM.;BS.;CEC.;TEB.;HA.;(SOM).	BS.;K.;Na.;TEB.		ODM.;C
	negative			ODM.		pH.;BS.;TEB.;Ca.;K
Mg	positive			Mg.;TEB.;SOM.;(C.;BS).		ODM.;SOM.;C
	negative		FA.	ODM.;N.		BS.;TEB.;Ca.;Mg
K	positive	N.;(SOM).	pH.;(BS).	BS.;Mg.;TEB.	pH	ODM.;C
	negative					
Na	positive				BS.;TEB	
	negative					
Cation Exchange Capacity (CEC)	positive	ODM.;SOM.;C.;N.	ODM.;Ca.;TEB.;SOM.;C.;HA.	HA.	SOM.;HA.;FA.;C	(P)
	negative					
P	positive			FA.	ODM.;HA.;FA.;N	(CEC)
	negative					
Soil Organic Matter (SOM)	positive	ODM.;CEC.;C.;N.;HA.;FA.;(K).	ODM.;CEC.;C.;(Ca.;TEB.;pH.;N.;FA).	K.;C.	CEC.;HA.;FA.;C	C
	negative			N		pH.;Mg.
Humic Acid (HA)	positive	SOM.;C.;FA.	CEC.;Ca.;TEB.	CEC.	ODM.;CEC.;P.;SOM.;FA	C
	negative					N
Fulvic Acid (FA)	positive	SOM.;C.;HA.	(SOM).	P	ODM.;CEC.;P.;SOM.;HA.	
	negative		Mg.			
Humin	positive				pH	
	negative					
C	positive	CEC.;SOM.;HA.;FA.;(N).	ODM.;CEC.;SOM.;N.	SOM.;(K).	CEC.;SOM.	SOM.;HA.
	negative			N		BS.;TEB.;Ca.;Mg.;K
N	positive	ODM.;CEC.;K.;SOM.;(C).	C.;(SOM).	K.;SOM.;C.	ODM.;P	Humin
	negative					

TABLE: 6.6.1 c

Principal Component Analysis Tree Groups

Correlation (p = < 0.05) of Soil parameters

Exotic deciduous trees show positive correlations between the fulvic fraction and soil organic matter and carbon. A strong negative correlation exists at this soil level between fulvic acid and magnesium.

The fire trees display a positve correlation with phosphorus at the lowest soil level.

There are little differences with regard to positive correlations between pH and base saturation, exchangeable bases T.E.B., and calcium under all tree groups and at all soil depth levels.

Magnesium however shows correlation differences between tree groups.

At the upper soil level magnesium is positively correlated with T.E.B. and potassium under fire trees, whereas a negative correlation exists under both indigenous and exotic deciduous trees between magnesium and C.E.C., T.E.B. and calcium.

The strong positive correlations under fire trees persist between magnesium and base saturation, T.E.B., sodium, potassium, soil organic matter and carbon at the mid soil level, and base saturation, T.E.B., sodium and potassium at the lowest soil level.

A negative correlation exists under fire trees at the mid soil level between magnesium and phosphorus.

At both lower soil levels, few correlations exist for magnesium under both, indigenous and exotic deciduous trees.

The exotic deciduous trees show a negative correlation between magnesium and the fulvic acid fraction and a positive, but insignificant correlation at 93 %; p = < 0.1 with phosphorus at the lowest soil level.

6.6.1.3 Linear regression analysis.

Figures 6.6.1 a-c show the regression analyses for the dependent parameters C.E.C. and T.E.B., at each soil level and for each group. At each soil strata, both the indigenous and the exotic deciduous trees show a positive linear regression. Under both associations, increases of C.E.C. generally relate to simultaneous increases of the amounts of exchangeable bases.

The influence of pyrophanerophytes is shown by a zero regression slope at the upper soil level and a negative slope at the lowest soil level.

This supports earlier suggestions on soil nutrient extraction (see 6.3.1; 6.4.1; 6.5). Differences of the exchange capacity under pyrophanerophytes must primarily be associated with exchangeable hydrogen and aluminium, since they show either no effect, or have a negative effect on exchangeable cations. Since the amounts of the exchangeable bases are within the range of those of the mineral substrate (Fig. 6.4.1c,d) the release of organic material with exchange capacity seems to serve primarily as a carrier of acidity, which facilitates with the decomposition of mineral nutrients.

Figure 6.6.1.a

P.C.A. groups; Regression at 0 - 1 cm
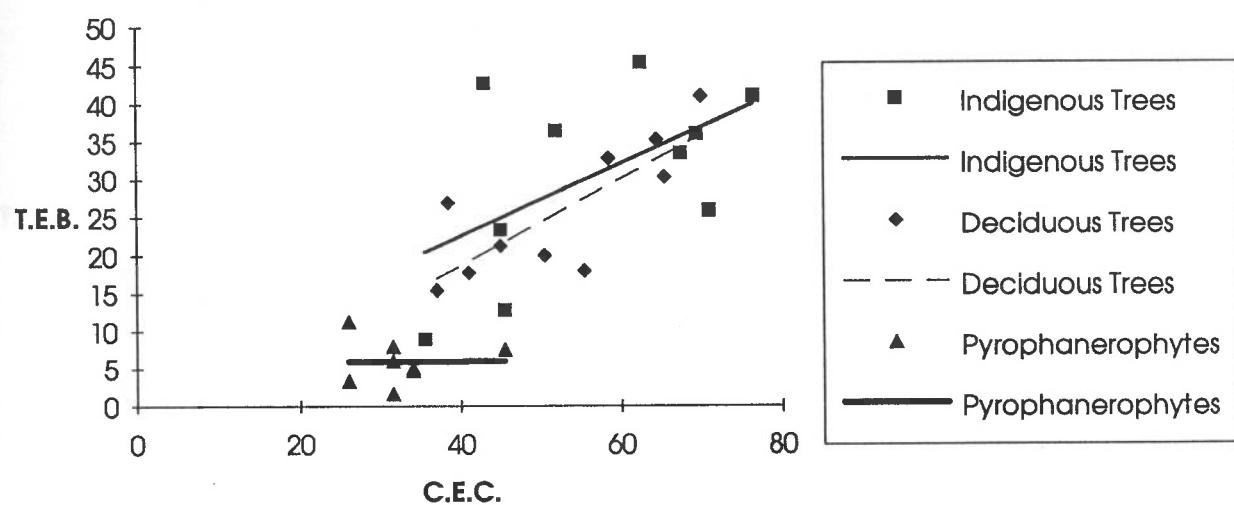
Figure 6.6.1.b

P.C.A. groups; Regression at 7 - 8 cm
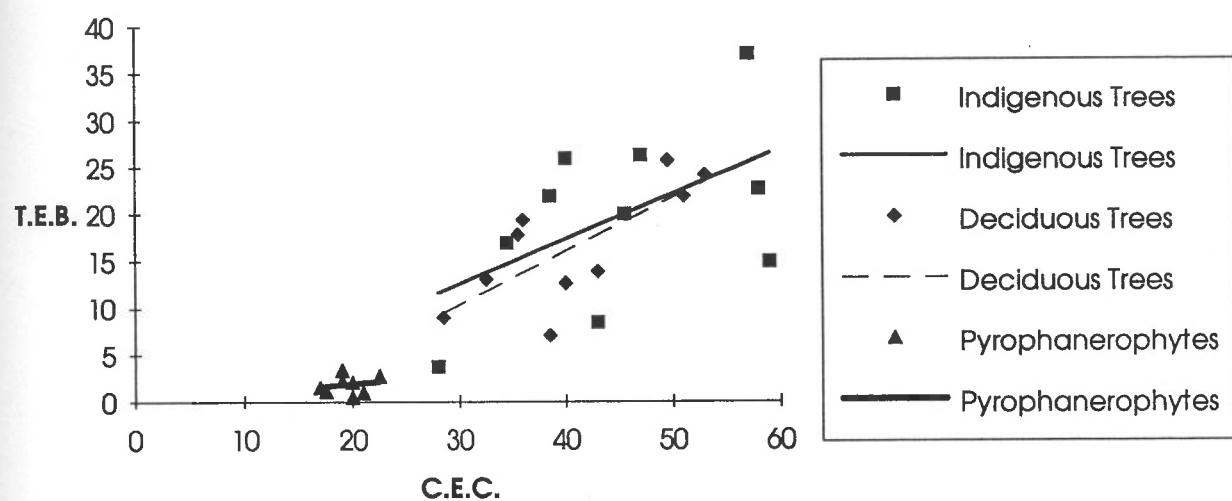
Figure 6.6.1.c

P.C.A. groups; Regression at 14 - 15 cm
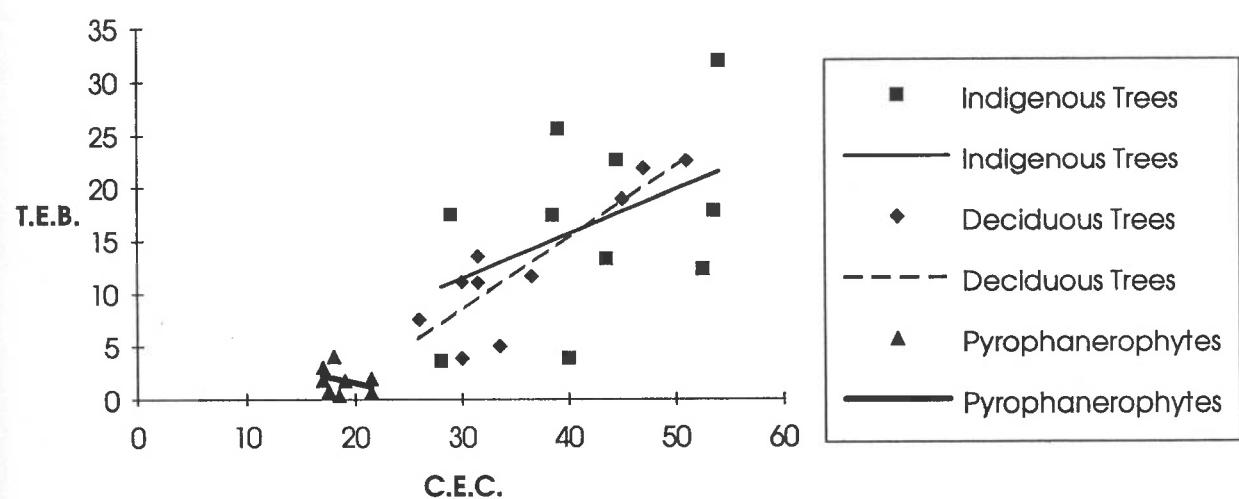
6.6.2.2 Dendrogram tree groups:

Significant correlations of soil parameters:

comparison between groups.

The correlations of soil parameters of the C.A. tree groups allow an insight into the range of nutrient cycling variations that were responsible for the tree grouping.

At the upper soil level, these differences result from a negative correlation of the C.E.C., the soil organic matter and the humin fraction with the pH level and the base saturation under trees of the "indigenous" group. This correlation is absent in the "deciduous" group and an additional difference relates to the positive correlation of nitrogen with magnesium and the negative correlation of nitrogen with potassium and phosphorus.

At the mid soil level the same trend continues in that carbon content and humic acid is negatively correlated with the pH level and the base saturation. Nitrogen is positively correlated with organic matter, C.E.C., humic acid and carbon under trees of the "deciduous" group.

Under trees of the "indigenous" group nitrogen is positively correlated with soil organic matter, humin and carbon, but negatively with the base saturation.

At the lowest soil depth the differences are slight and might be based on the positive correlation of C.E.C. with humin under the "indigenous" group and positive correlations of C.E.C. with fulvic acid and a negative correlation of the latter with the pH level under the trees of the "deciduous" group.

The exchangeable bases are positively correlated to the base saturation under most tree groups and soil levels. There is no correlation for these parameters under the myrtax group at the upper two soil levels.

The main difference between the *Pinaceae* and the myrtax group is that the C.E.C. under the myrtax group is positively correlated to soil organic matter and the humic extracts at the mid- and lowest soil depths. In addition, at the mid soil depth humic acid is positively correlated to calcium and negatively to magnesium and there is a positive correlation between carbon and nitrogen. These are some of the characteristics that have been shown to be typical for the indigenous and deciduous associations, at significantly higher means compared to the trees of the myrtax group (sect. 6.4).

The origins of the myrtax group are diverse, as are the ecological adaptations of its component species. (*Cryptomeria japonica* is not a pyrophanerophyte.)

The same is true for the "indigenous" and the "deciduous" groups.

Results therefore reflect the diversity of cycling strategies within temperate forests.

Individual nutrient cycling strategies, that cover a broad range, are indicated by the ordinations (see sect. 6.1.& 6.2) and evidenced by the distinct clustering of the Pinatae and the eucalypts. In order to statistically verify individual strategies of species, a design is required that allows for the sampling of a far higher number of replicate species, all growing on a homogeneous substrate.

However, these soil parameter correlation differences give an indication on the extent of nutrient cycling strategies within the temperate forest biomes.

The main reason for the grouping of trees into either the "indigenous" - or the "deciduous" group is associated with quantitative species specific differences in the cycling of nutrients (see section 6.6.2.3).

The association of species, which form either mull and mor humus with both "indigenous" and "deciduous" groups gives an insight into individual quantitative nutrient cycling differences, that are independent of substrate quality within indigenous and deciduous forest ecosystems.

CORRELATION CONFIDENCE 95%	pos./neg.	Indigenous group 0-1 cm	Deciduous group 0-1 cm	Fire Tree group 0-1 cm	Myrtaceae 0-1 cm	Pinaceae 0-1 cm
Moisture content air to oven dry {ODM}	positive					
	negative					
pH	positive	B.S.	BS.;TEB;Ca	TEB.;Ca.;HA.	TEB.HA	
	negative	CEC.;SOM.;Humin;C				
Base Saturation {BS}	positive	pH;TEB.;Ca	pH.;TEB.;Ca	BS.,TEB.;Ca.;K.;P	BS.;P	BS.,TEB.;Ca.;Mg.;K.;P
	negative	CEC.;SOM.;Humin				
Total exchangeable Bases {TEB}	positive	BS.;Ca	pH.;BS.;Ca	pH.;TEB.;Ca.;Mg.;K.;P	pH.	pH.;TEB.;Ca.;Mg.;K.;
	negative		Mg			
Ca	positive	BS.;TEB.	pH.;BS.;TEB.;	ODM.;pH.;BS.;Ca.;Mg.;K.;P	ODM.;Ca.	pH.;BS.;Ca.;Mg.;;
	negative		Mg			
Mg	positive		N	ODM.,pH.;BS.;TEB.;Mg.;K.;P	TEB.	pH.;BS.;TEB.;Mg
	negative		TEB.;Ca			
K	positive		N	BS.,TEB.;Ca.;K	(K.;N)	pH.;BS.;TEB.;Ca.;K
	negative					
Na	positive	FA.	HA.;C	pH.;BS.;TEB.;Ca.;Mg.;P	(Mg)	pH.;BS.;Mg
	negative			N		
Cation Exchange Capacity {CEC}	positive	Humin	(Humin)	SOM.;HA.;Humin.;C		Humin
	negative	pH.;BS.				
P	positive		N	pH.;BS.;TEB.;Ca.;Na.	pH	pH.;
	negative					
Soil Organic Matter {SOM}	positive	HA.;Humin;C	Humin;C	CEC.;HA.;Humin.;C	FA.;Humin (K)	HA.;Humin;C
	negative	pH.;BS.;				
Humic Acid {HA}	positive	Na.;SOM.;F.A.;C	(Mg);Na.;C	ODM.;CEC.;SOM.Humin.;C	ODM.	SOM.;C
	negative					
Fulvic Acid {FA}	positive	Na.;HA.;C		N	SOM.;Humin;C	
	negative					
Humin	positive	CEC.;SOM.;C	(CEC);SOM.;	CEC.;SOM.;HA.;C	SOM.;FA	CEC.;SOM.
	negative	pH.;BS.;				
C	positive	SOM.;HA.;FA.;Humin	Na.;SOM.;HA.;	CEC.;SOM.;HA.;Humin	FA	SOM.;HA.;Humin
	negative	pH.	Mg.			
N	positive		K.;P	Na.;FA	(Mg)	
	negative					

Correlation (p = < 0.05) of Soil parameters   **TABLE: 6.6.2 a**   Dendrogram Tree Groups

CORRELATION	pos./neg.	Indigenous group 7-8 cm	Deciduous group 7-8 cm	Fire Tree group 7-8 cm	Myrtaceae 7-8 cm	Pinaceae 7-8 cm
CONFIDENCE 95%						
Moisture content air to oven dry {ODM}	positive	CEC.;Humin	CEC.;SOM.;HA.;C	CEC.;P.;SOM.;HA.;C.;N	CEC.;P.;N	Na.;C
	negative					BS.;Ca
pH	positive	BS.;TEB.;Ca.	BS.;TEB.;Ca.	BS.;TEB.;Mg.;K.;		Na
	negative	HA.;C		pH.;TEB.;Mg.;K.	Na	TEB.;Ca.;Mg
Base Saturation {BS}	positive	pH.;TEB.;Ca.	pH.;TEB.;Ca	M.;pH.;BS.;Ca.;Mg.;K.;Humin	Humin;C	ODM.;C
	negative	SOM.;HA.;C.;N	(FA)			BS.;Ca.;Mg.
Total exchangeable Bases {TEB}	positive	pH.;BS.;Ca	pH.;BS.;Ca.	M.;BS.;TEB.;Humin	M.;SOM.;HA.;(Humin);C.;N	BS.;TEB.;Mg
	negative					ODM.;C
Ca	positive	pH.;BS.;TEB.	pH.;BS.;TEB.	pH.;BS.;TEB.;K.;Humin		BS.;TEB.;Ca.;
	negative				CEC.;(HA)	C
Mg	positive	Na.;CEC		pH.;BS.;TEB.;K.;Humin		
	negative				FA	ODM.
K	positive			pH.;BS.;TEB.;Mg.;Humin.		
	negative	C			BS	pH
Na	positive	Mg		Humin;C		
	negative					
Cation Exchange Capacity {CEC}	positive	M.;ODM.;SOM.;(HA).;C	ODM.;SOM.;Humin;C.;N	M.;ODM.;P.;HA.;C.;N	ODM.;P.;SOM.;HA.;C.;N	HA.
	negative	Mg		ODM.;CEC.;FA.;N	Mg	N
P	positive				ODM.;CEC.;SOM.;(HA).;C.;N	SOM.
	negative	CEC.;HA.;Humin;C.;N	ODM.;CEC.;HA.;Humin;C.;N	M.;ODM.;TEB.;CEC.;HA.;Humin;C.;N	M.;Ca.;CEC.;CEC.;PHA.;C.;N	N
Soil Organic Matter {SOM}	positive	BS.	ODM.;SOM.;N	M.;ODM.;CEC.;SOM.;N	M.;Ca.;CEC.;(P).;SOM.;C.;N	ODM.
	negative	CEC.;SOM.;C			(Mg)	
Humic Acid {HA}	positive	pH.;BS.		P	K	
	negative					
Fulvic Acid {FA}	positive		(BS)		TEB.;(Ca).;	
	negative					
Humin	positive		CEC.;SOM.;C	M.;BS.;TEB.;Ca.;Mg.;K.;Na.;SOM.;C	M.;Ca.;CEC.;P.;SOM.;HA.;N	BS.;Ca.;Mg
	negative	ODM.;SOM.;N	ODM.;CEC.;SOM.;Humin;N	M.;ODM.;Na.;CEC.;SOM.;HA.;Humin;N		ODM.
C	positive					
	negative	Na.;CEC.;SOM.;HA.;N	CEC.;SOM.;HA.;C	M.;ODM.;CEC.;P.;SOM.;HA.;C	M.;ODM.;Ca.;CEC.;P.;SOM.;HA.;C	BS.;Ca.;Mg
N	positive	pH.;BS.				SOM.;HA
	negative	SOM.;Humin;C		TEB.;Ca.;CEC.;SOM.;HA.;Humin;C.;N	Ca.;SOM.;HA.;C.;N	
Moisture content field to air dry {M}	positive	BS.				
	negative	CEC				

TABLE: 6.6.2 b

Dendrogram Tree Groups

Correlation (p = < 0.05) of Soil parameters

CORRELATION CONFIDENCE 95%	pos./neg.	Indigenous group 14-15cm	Deciduous group 14-15cm	Fire Tree group 14-15cm	Myrtaceae 14-15cm	Pinaceae 14-15cm
Moisture content air to oven dry (ODM)	positive	CEC.;SOM.;Humin.;C.;N	CEC.;SOM.;FA.;N	CEC.;P.;HA.;FA.;N	P.;HA.;FA.;N	BS.;TEB.;Ca.;Mg.;K.
	negative					Mg
pH	positive	BS.;TEB.;Ca.;	BS.;TEB.;Ca			SOM.
	negative		FA		K.;Humin	
Base Saturation (BS)	positive	pH.;TEB.;Ca	pH.;TEB.;Ca.	TEB.;Ca.;Mg.;K.;Na	TEB.;Na.	TEB.;Ca.;Mg.;K
	negative					ODM.;C
Total exchangeable Bases (TEB)	positive	pH.;BS.;Ca.	pH.;BS.;Ca.	BS.;Ca.;Mg.;K.;Na.	BS.;Na	BS.;Ca.;Mg.;K
	negative					ODM.;C
Ca	positive	pH.;BS.;TEB.	pH.;BS.;TEB	BS.;Ca.;K.;Na		BS.;TEB.;Mg.;K
	negative					ODM.;C
Mg	positive			BS.;TEB.;K		pH.;BS.;TEB.;Ca.;K
	negative					ODM.;SOM.;C
K	positive	SOM.;C		BS.;TEB.;Ca.;Mg.;(Na)		BS.;TEB.;Ca.;Mg
	negative				pH	ODM.;C
Na	positive	HA		BS.;TEB.;Ca.;(K)	BS.;TEB	
	negative					
Cation Exchange Capacity (CEC)	positive	ODM.;Humin.;C.;N	ODM.;SOM.;FA.;C.;N	ODM.;SOM.;HA.;FA.;C	SOM.;HA.;FA.;C	(P)
	negative	P				
P	positive	CEC		ODM.;FA.;N	ODM.;HA.;FA.;N	(CEC)
	negative					
Soil Organic Matter (SOM)	positive	ODM.;K.;HA.;FA.;Humin.;C.;N	ODM.;CEC.;FA.;Humin;C.;N	CEC.;HA.;Humin;C	CEC.;HA.;FA.;C	C
	negative					pH.;Mg.
Humic (HA)	positive	Na.;SOM.;FA.;C	C	ODM.;CEC.;SOM.;Humin.;C.	ODM.;CEC.;P.;SOM.;FA	C
	negative					
Fulvic (FA)	positive	SOM.;HA.;C	ODM.;CEC.;SOM.	ODM.;CEC.;P.	ODM.;CEC.;P.;SOM.;HA.	
	negative		pH			
Humin	positive	ODM.;CEC.;SOM.;C.	SOM.;C	SOM.;HA.	pH	
	negative					N
C	positive	ODM.;K.;CEC.;SOM.;HA.;FA.;Humin;N	(CEC).;SOM.;HA.;(HA).;Humin;N	CEC.;SOM.;HA.;Humin	CEC.;SOM.	SOM.;HA.
	negative					BS.;TEB.;Ca.;Mg.;K
N	positive	ODM.;CEC.;SOM.;Humin;C	ODM.;CEC.;SOM.;C	ODM.;P.	ODM.;P	
	negative					Humin

TABLE: 6.6.2 c

Correlation (p = < 0.05) of Soil parameters   Dendrogram Tree Groups

6.6.2.3 Linear regression analyses.

Figures 6.6.2 a-c show the regression analyses for the parameters, C.E.C. and T.E.B., at each soil level and for each group.

The analyses of variance (Section 6.3.2) established that there were significant differences between the three main groups at all depths for the both parameters, which are apparent from the distance of the regression lines from each other.

The regression results on the dendrogram based tree groupings show the tree specific vigours of nutrient cycling. The level of the "indigenous" group exceeds by far that of the mineral base parameters and shows a high efficiency in the creation of nutrient storage. The "indigenous" group shows a slightly negative regression slope at the upper most soil level, a zero slope at the mid soil level and a slightly positive slope at the lowest soil level. This suggests that this particular association primarily increases the exchange capacity. There is an initial excess of the exchange capacity at the upper strata (0-1 cm). The T.E.B. saturate the exchange capacity with soil depth.

The "deciduous" group shows a positive regression slope at the upper soil level, a negative slope at the mid soil level and a slightly positive one at the lowest soil level. At the upper level, increases of C.E.C. relate to increases of T.E.B., while the absolute amounts are less than those of the "indigenous" group. The cycling of nutrients is well adjusted to the simultaneous creation of nutrient storage space. However, at the mid soil level, increases of nutrient storage relate to decreases of exchangeable bases and suggests a net immobilization of nutrients by the biomass. At the lowest soil level, this trend is again reversed, and increases of the C.E.C. are related to slight increases of the T.E.B., but again at a lower level, compared to the trees of the "indigenous "group.

The influence of the sub-groups of the "pyrophanerophyte" group is shown by a slightly negative regression slope at the upper soil level under the Pinaceae and a slightly positive slope under the influence of the myrtax group. At both deeper soil levels the slopes are zero for both groups and within the range of the mineral contribution of exchangeable bases. These results support suggestions made for the pyrophanerophyte group in section 6.0.0.3.

> **The release of organic material with exchange capacity seems to serve primarily as a carrier of acidity, which facilitates the decomposition of clay minerals and mineral humic compounds for the acquisition of nutrients.**

Figure 6.6.2.a

Dendrogram groups; Regression at 0 - 1 cm
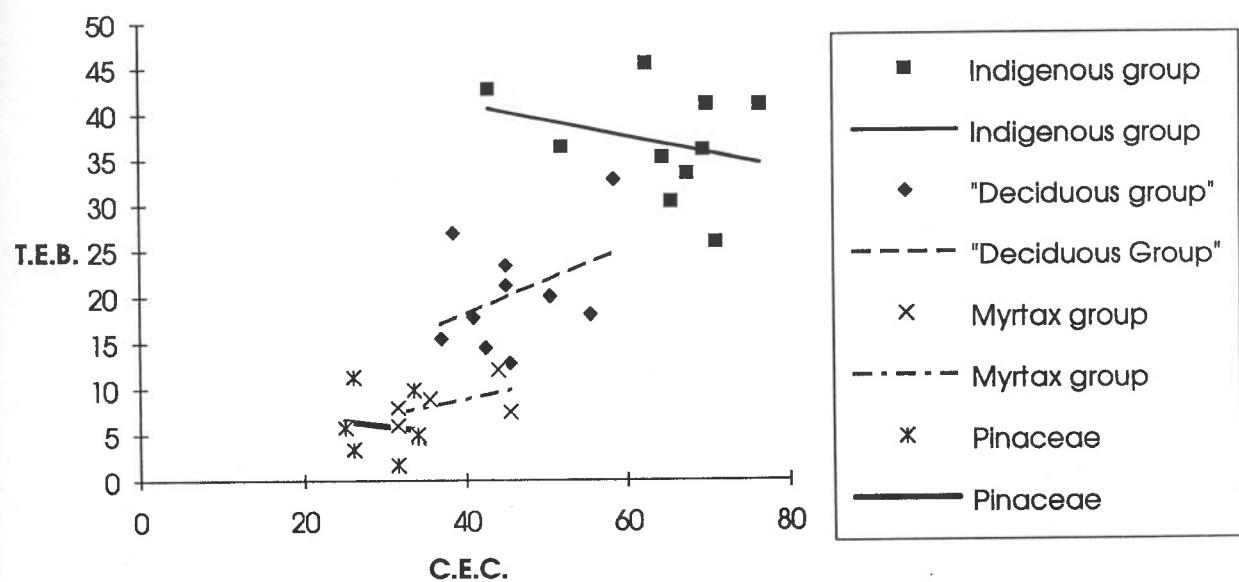
Figure 6.6.2.b

Dendrogram groups; Regression at 7 - 8 cm

Figure 6.6.2.c

Dendrogram groups; Regression 14-15 cm
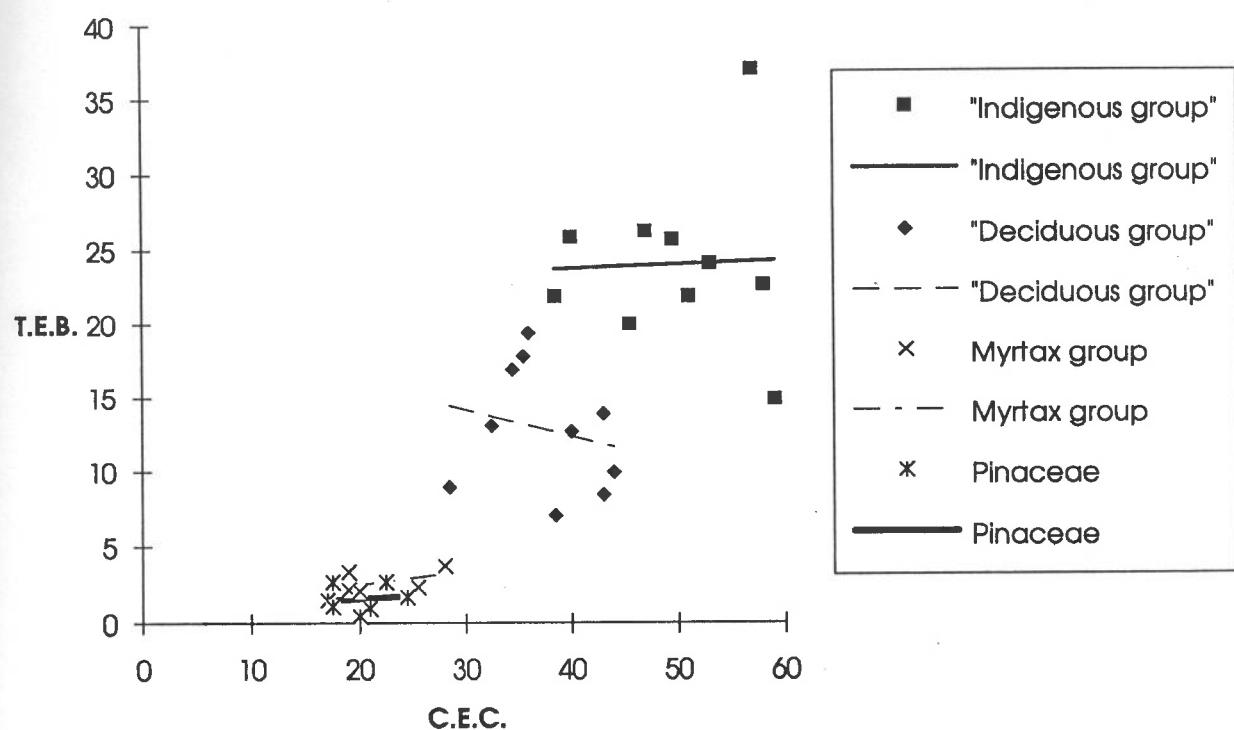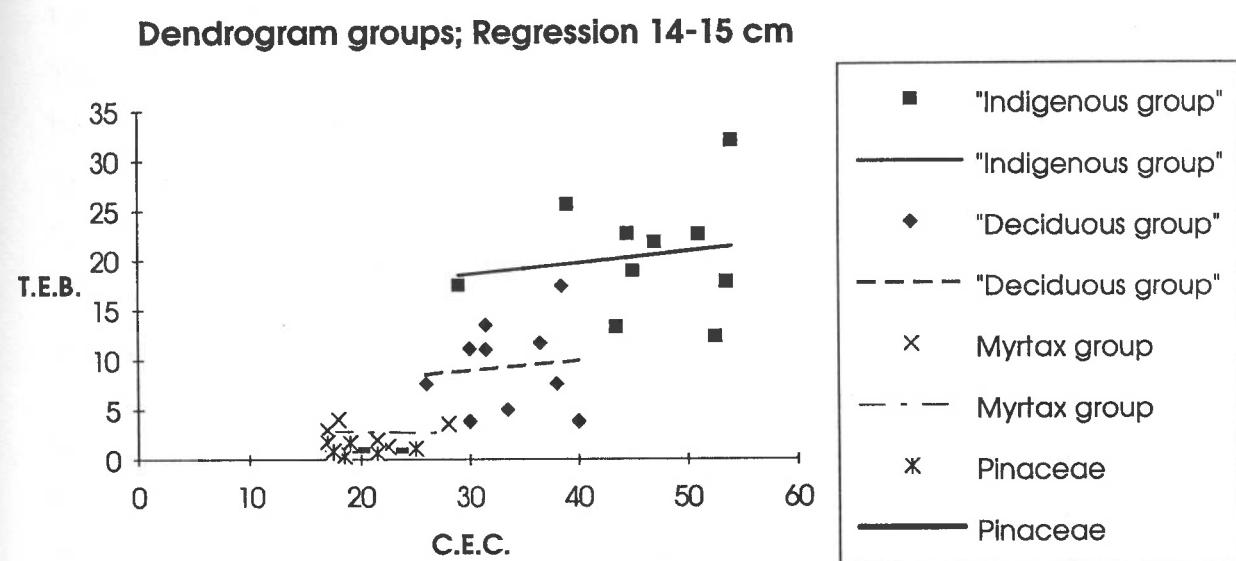
6.6.1.4 P.C.A. tree groups:

Significant within group correlations of soil parameters with soil depth.

Tables 6.6.1 d - f allow a direct comparison for each tree group of the significant correlations (p = < 0.05) with soil depth.

The rather compressed range of most soil parameters under the pyrophanerophytes from both, P.C.A. ordination and from the cluster analysis, has obviously had an influence on the high number of obvious correlations between soil parameters within the fire tree group and its sub-groups.

Under the influence of <u>indigenous trees,</u> **soil organic matter** is associated with C.E.C., humic acid, carbon and nitrogen at all soil depths and with fulvic acids at the upper and the lowest soil depth.

The **pH levels** are associated with base saturation, calcium and the exchangeable bases at all soil depths.

The **humic acid fraction** is associated with sodium in the upper soil section, with C.E.C., carbon and nitrogen in the upper and mid sections of the soil A-horizon and with the fulvic acid fraction and carbon at the lowest soil A-horizon section.

The **fulvic acid fraction** is associated with carbon, nitrogen, sodium, humic acid and soil organic matter at the upper soil level, with potassium and sodium at the mid soil level and with soil organic matter, carbon and the humic acid fraction at the lowest soil level.

Soil **nitrogen** contents are associated with carbon, soil organic matter, humic acid and fulvic acid fractions in the upper and mid soil levels and with C.E.C. soil organic matter at the mid and lowest soil level.

Under the influence of the <u>exotic deciduous angiosperms,</u> the **soil organic matter** is associated with C.E.C., carbon and soil moisture at all soil levels. Soil organic matter is associated with nitrogen and base cations particularly at the mid and lowest soil level.

The **pH level** is positively correlated with the base saturation and the exchangeable bases, in particular with calcium, at all soil levels, with potassium at the upper and the lowest soil level and with sodium at the mid soil level.

The **exchangeable bases** are positively correlated to the C.E.C., which in turn is positively correlated with soil organic matter throughout the soil A-horizon.

The **humic acid fraction** is increasingly associated with exchangeable nutrients with soil depth. It is correlated with nitrogen at the mid soil level and with the exchangeable bases, in particular calcium and with the C.E.C. at the lowest soil level.

Soil **nitrogen** is associated with carbon at the lowest soil level and with C.E.C., carbon, soil organic matter, humic acid and soil moisture at the mid soil level.

Under the influence of <u>fire trees</u> **soil organic matter** is associated with C.E.C., carbon and nitrogen at the upper soil level, with carbon, magnesium and sodium at the mid soil level, with carbon and potassium at the lowest soil level, where SOM is negatively correlated with nitrogen.

The **pH level** is associated with the base saturation, the exchangeable bases, calcium and potassium at the upper and the mid soil depth level, and with calcium at the lowest soil level.

The limited amounts of **phosphorus** are positively correlated at the upper soil level to the pH level, the base saturation and the exchangeable bases, calcium and potassium and to fulvic acid at the lowest soil level. Phosphorus is negatively correlated with magnesium at the mid soil level.

The **humic acid fraction** is associated with carbon at the upper soil level and with C.E.C. at the lowest soil level.

The **fulvic acid fraction** is associated with nitrogen at the upper and the mid soil level and with phosphorus at the lowest soil level.

A positive correlation of **nitrogen** with soil organic matter and **carbon** changes into a negative correlation with soil depth.

The results will be discussed in the section 6.8 and chapter 8.

CORRELATION	pos./neg.	Indigenous trees	Indigenous trees	Indigenous trees
CONFIDENCE 95%		0-1 cm	7-8 cm	14-15cm
Moisture content air to oven dry {ODM}	positive		CEC.	CEC.;SOM.;N.;(C).
	negative			
pH	positive	BS.;Ca.;TEB.;(P)	BS.;Ca.;TEB.;	BS.;Ca.;TEB.
	negative			
Base Saturation {BS}	positive	pH.;Ca.;TEB.	pH.;Ca.;TEB.	pH.;Ca.;TEB.;(P).
	negative			
Total exchangeable Bases {TEB}	positive	pH.;BS.;Ca.	pH.;BS.;Ca.	pH.;BS.;Ca.
	negative	Mg.		
Ca	positive	pH.;BS.;TEB.	pH.;BS.;TEB.	pH.;BS.;TEB.
	negative	Mg.		
Mg	positive			
	negative	CEC.;Ca.;TEB.		
K	positive			
	negative		FA.	N.;(SOM).
Na	positive	HA.;FA.	CEC.;(C.;N)	
	negative			
Cation Exchange Capacity {CEC}	positive	SOM.;C.;HA.	ODM.;Na.;SOM.;C.;N.;HA.;(FA).	ODM.;SOM.;C.;N.
	negative	Mg		
P	positive	(pH).		
	negative			
Soil Organic Matter {SOM}	positive	CEC.;C.;N.;HA.;FA.	CEC.;C.;N.;HA.	ODM.;CEC.;C.;N.;HA.;FA.;(K).
	negative			
Humic Acid {HA}	positive	CEC.;Na.;SOM.;C.;N.;FA.	CEC.;SOM.;C.;N.	SOM.;C.;FA.
	negative			
Fulvic Acid {FA}	positive	Na.;SOM.;C.;N.;HA.	ODM.;K.;Na.;(N.;CEC).	SOM.;C.;HA.
	negative			
Humin	positive			
	negative			
C	positive	CEC.;SOM.;N.;HA.;FA.	CEC.;SOM.;N.;HA.	CEC.;SOM.;HA.;FA.;(N).
	negative			
N	positive	SOM.;C.;HA.;FA.	CEC.;SOM.;C.;HA.;(FA).	ODM.;CEC.;K.;SOM.;(C).
	negative			
Moisture content field to air dry {M}	positive			
	negative			

TABLE: 6.6.1 d

Correlation (p = < 0.05) of Soil parameters

Principal Component Analysis Tree Groups

CORRELATION	pos/neg.	Deciduous trees	Deciduous trees	Deciduous trees
CONFIDENCE 95%		0-1 cm	7-8 cm	14-15cm
Moisture content air to oven dry {ODM}	positive		CEC.;Ca.;TEB.;SOM.;C.;N.;(NA).	CEC.;Ca.;SOM.;C.;(HA).
	negative			
pH	positive	BS.;Ca.;K.;TEB	BS.;Ca.;Na.(TEB).	BS.;Ca.;K.;TEB.;(SOM).
	negative			
Base Saturation {BS}	positive	pH.;Ca.;K.;TEB	pH.;Ca.;K.;TEB.	pH.;Ca.;TEB.;(K).
	negative			
Total exchangeable Bases {TEB}	positive	pH.;ODM.;BS.;CEC.;Ca.;K.	ODM.;BS.;CEC.;Ca.;K.;Na.	pH.;BS.;CEC.;Ca.;HA.
	negative	Mg.		
Ca	positive	pH.;ODM.;BS.;CEC.;K.;TEB	ODM.;BS.;CEC.;K.;Na.;TEB.	pH.;ODM.;BS.;CEC.;TEB.;HA.;(SOM).
	negative	Mg.		
Mg	positive			
	negative	CEC.;Ca.;K.;TEB.		FA.
K	positive	pH.;BS.;Ca.;TEB	BS.;Ca.;TEB.	pH.;(BS).
	negative	Mg.		
Na	positive		pH.;Ca.;TEB.;(ODM.;CEC.;SOM.;N)	
	negative			
Cation Exchange Capacity {CEC}	positive	ODM.;Ca.;TEB.;(SOM.).;C	ODM.;Ca.;Na.;TEB.;SOM.;C.;N.	ODM.;Ca.;TEB.;SOM.;C.;HA.
	negative	Mg.		
P	positive			
	negative			
Soil Organic Matter {SOM}	positive	(CEC).;ODM.;C.;(HA).	ODM.;CEC.;C.;N.	ODM.;CEC.;C.;(Ca.;TEB.;pH.;N.;FA).
	negative			
Humic	positive	(SOM.;C)	N	CEC.;Ca.;TEB.
Acid {HA}	negative			
Fulvic	positive			(SOM).
Acid {FA}	negative	Mg.		Mg.
Humin	positive			
	negative			
C	positive	ODM.;CEC.;SOM.;(HA).	ODM.;CEC.;SOM.;N.	ODM.;CEC.;SOM.;N.
	negative			
N	positive	ODM.	ODM.;CEC.;SOM.;C.;HA.;(Na).	C.;(SOM).
	negative			
Moisture content field to air dry {M}	positive			
	negative			

Correlation (p = < 0.05) of Soil parameters   TABLE: 6.6.1 e   Principal Component Analysis Tree Groups

CORRELATION CONFIDENCE 95%	pos./neg.	Pyro-phanerophytes 0-1 cm	Pyro-phanerophytes 7-8 cm	Pyro-phanerophytes 14-15cm
Moisture content air to oven dry {ODM}	positive	(HA)		
	negative			
pH	positive	BS.;Ca.;K.;TEB.;P	BS.;Ca.;K.;TEB.;(Mg)	Ca.;Mg.;K.;(TEB.;BS).
	negative			Ca.
Base Saturation {BS}	positive	pH.;Ca.:(Mg).;K.;TEB.;P.	pH.;M.;Mg.;K.;TEB.;(Na.;Ca).	Mg.;Na.;TEB.;(Ca.;pH.;K).
	negative			(ODM).
Total exchangeable Bases {TEB}	positive	pH.;BS.;Ca.;Mg.;K.;P.	pH.;BS.;Ca.;Mg.;K.	BS.;Mg.;K.;Na.;(Ca).
	negative			(ODM).
Ca	positive	pH.;(BS.;Mg).;K.;TEB.;P.	pH.;TEB.;(BS)	pH.;(BS.;TEB).
	negative			ODM.
Mg	positive	(BS.;Ca.;N).;K.;TEB.	M.;BS.;K.;Na.;TEB.;SOM.;C.;(pH).	BS.;K.;Na.;TEB.
	negative		P	ODM.
K	positive	pH.;BS.;Ca.;Mg.;TEB.;P.	pH.;BS.;Mg.;TEB.	Mg.;TEB.;SOM.;(C.;BS).
	negative			ODM.;N.
Na	positive	N	Mg.;SOM.;C.;(BS).	BS.;Mg.;TEB.
	negative			
Cation Exchange Capacity {CEC}	positive	SOM.		HA.
	negative			
P	positive	pH.;BS.;Ca.;K.;TEB.	Mg.;(M).	FA
	negative			
Soil Organic Matter {SOM}	positive	CEC.;C.;N.;(FA)	Mg.;Na.;C.	K.;C.
	negative			N
Humic Acid {HA}	positive	C		CEC.
	negative			
Fulvic Acid {FA}	positive	(SOM).;N.	N	P
	negative			
Humin	positive			
	negative			
C	positive	SOM.;HA.	Mg.;Na.;SOM.	SOM.;(K).
	negative			N
N	positive	Na.;SOM.;FA.;(Mg).	FA.	K.;SOM.;C.
	negative			
Moisture content field to air dry {M}	positive		BS.;Mg.	
	negative		(P)	

TABLE: 6.6.1 f   Principal Component Analysis Tree Groups

Correlation (p = < 0.05) of Soil parameters

6.6.2.3 Dendrogram tree groups;

Significant within group correlations with soil depth.

The basis for the association of trees with either the "indigenous" or the "deciduous" groups has been discussed in section 6.6.2.2. A comparison with soil depth is therefore superfluous.

The division of the "pyrophanerophyte" group into the *Pinaceae* and the myrtax group allows for a comparison of taxonomically based, group specific effects on the relationship of the soil parameters.

The soil parameter correlations of the *Pinaceae* are interpretable in this way. The myrtax group is composed of *Myrtaceae* (*Eucalyptus* and *Kunzea*) and the *Taxodiaceae*, *Cryptomeria japonica*.

Under the *Pinaceae* the C.E.C. is positively correlated with the humin fraction at the upper soil level (see Tables 6.6.1; 6.6.2 a - c). No further correlations with soil depth suggests that the C.E.C. is predominantly mineral based within the soil A-horizon. This suggestion was made earlier, when the C.E.C. measurements were compared with the mineral soil C.E.C. contributions, measured by Tomlinson and Leslie (1977). (sect. 6.4.1)

The limited soil parameter relationship of the C.E.C. is further illustrated by a negative correlation of **carbon**, with calcium, magnesium and base saturation at the mid soil depth level and with calcium, magnesium, potassium, the exchangeable bases and the base saturation at the lowest soil depth level.

Considering the latter, it is not surprising that there is a further negative correlation of **soil organic matter** content with magnesium and the pH level at the lowest soil depth. Soil organic matter is positively correlated with **humic acid** at the upper - and mid soil level and with carbon at the lowest soil level. Humic acid is positively correlated with carbon at the upper - and at the lowest soil level.

At the mid soil depth level there is a negative correlation of **nitrogen** with soil organic matter and with humic acid, as well as with humin at the lowest soil horizon.

These correlations show clearly that there is no detectable activity of nutrient cycling under the *Pinaceae* and that soil organic material in the soil A-horizon is associated with the depletion of nutrient cations and nitrogen.

6.7.0.0 Alternate Hypotheses

On the basis of the rejection of H_O 1 and H_O 2, the results of the ANOVA (sect. 6.3) and the correlation and regression analyses (sect. 6.6), further alternative hypotheses can be formulated.

The fact that trees forming mull humus were at the centre of the "indigenous" group suggested that there are species that cycle the nutrients at amplitudes of various intensities, and independent of the quality of the mineral substrate, in both indigenous and exotic deciduous forest ecosystems. Largest differences between the "indigenous" - and "deciduous" group were for C.E.C. and T.E.B. (figs. 6.3.2.c;d) and these parameteres are assumed to be responsible for the individual associations with groups.

The analysis of variance demonstrates that additional soil parameters are indicative of different intensities of nutrient cycling conditions, fuelled by species specific litter-loads, within the indigenous and the exotic deciduous forest ecosystems.

The following soil parameters were significantly different between the indigenous and deciduous trees in the "indigenous" group and the trees of mixed origin in the "deciduous" group:

... at all soil depth levels:

base saturation; total exchangeable bases; calcium; potassium; sodium; cation exchange capacity; organic matter; humic acid; carbon.

...only at the upper soil level: magnesium; fulvic acid.

...only at the mid soil level: field to air dry soil moisture; magnesium; nitrogen.

... only at the lowest soil level: ratio humic acid/fulvic acid

These differences verify that there is a wide range of individual nutrient cycling strategies (towards mull, moder, mor humus types) and amplitudes (vigours of nutrient cycling, leading to one or the other soil humus type) within a particular coherent forest ecosystem. This range secures the efficiency of nutrient cycling, spatial and temporal species dynamics, and the inertia of a forest ecosystem against detrimental external influences.

These effects can be described with the following hypothesis,

H_A 4 A) A wide range of species specific nutrient cycling strategies and nutrient cycling vigours is covered by indigenous species and exotic deciduous species within the particular forest ecosystem of origin.

The extent of this range, encompassing the particular indigenous and the exotic deciduous forest ecosystem is rather similar.

The nutrient cycling vigours or amplitudes towards one or the other soil humus type are therefore both species specific and

dependent on the quality of the mineral substrate.

The results of section 6.6 gave an insight into the correlations of parameters between tree group and soil depths that permit the formulation of the following additional alternate hypotheses for the:

Indigenous and Deciduous Forest Associations;

H_A 6 Under the influence of indigenous and exotic deciduous trees C.E.C. increases, and is positively correlated at various soil A-horizon depths with increases in soil organic matter, soil moisture and carbon.

H_A 7 Under the influence of indigenous and exotic deciduous trees increases in C.E.C. are correlated with increases in nitrogen and humic acids at lower soil A-horizon levels.

H_A 8 Under the influence of exotic deciduous trees, the exchangeable bases are positively correlated to the C.E.C., which in turn is positively correlated with soil organic matter throughout the soil A-horizon.

H_A 9 Under the influence of exotic deciduous trees and with soil depth in the A-horizon, the humic acid fraction is highly correlated with the storage of nitrogen and exchangeable cations.

H_A 10 Under indigenous and exotic deciduous trees, at the upper most soil level increases of C.E.C. and T.E.B. are negatively correlated with magnesium.

H_A 11 Under the influence of indigenous and exotic deciduous trees the soil A-horizon is subject to intensive bioturbation activities, leading to the incorporation of organic compounds and exchangeable nutrients.

H_A 12 The influence of indigenous and exotic deciduous trees is characterised by interactions that encourage nutrient cycling and nutrient storage.

Litter compositions show individual amplitudes of nutrient cycling, which are independent of mull - or moder forming litter qualities.

Pyrophanerophytes;

H_A 13 The influence of fire trees shows **no correlation** between **C.E.C.** and **nutrient cations**.

H_A 14 The influence of fire trees demonstrates **no correlation** between the **humic acid and the fulvic acid fractions** and the **exchangeable bases**.

H_A 15 There is no detectable activity of nutrient cycling under the *Pinaceae.*

A limited amount of soil organic material in the soil A-horizon is associated with humic acid and carbon, which is associated with a decreasing pH level and the depletion of nutrient cations and soil nitrogen.

H_A 16 The influence of fire trees on the soil is characterized by **nutrient extraction** and **nutrient storage decreases**, caused by the accelerated decomposition of soil nutrient stores.

6.8.0.0   Discussion:

Nutrient cycling strategies.

Tree species have evolved in both, northern and southern hemisphere temperate forest biomes that demonstrate different amplitudes, or efficiencies, of nutrient cycling towards one or the other soil humus type.

Litter inputs of species from both, indigenous and deciduous forest ecosystems, lead to high and medium increases of C.E.C. and T.E.B., while at the same time evolving, for example, a soil mull humus type (or a moder humus type).

Litter of the *Nothofagus* species contains high amounts of carbon and calcium, which has also been shown to be a general feature of *Fagus sylvatica* (Wittich, 1953; 1972). The *Nothofagus* litter initially resists decomposition and a considerable organic fraction could enrich the pool of humic substances. The combination of carbon and minerals creates a fertile mull humus with a high buffer capacity in the soil A-horizon.

Carbon compounds from species that produce readily decomposable litter are rapidly mineralised. On its own, such litter would lead to only limited increases of humic C.E.C. and nutrients from the mineral rich *Melicytus ramiflorus* litter (Enright and Ogden, 1987), amongst others could easily be lost to the system, if the nutrients can not attach to additional organic exchange sites.

The presence of tree litter, that somewhat resists decomposition has the potential, if within the mull to moder buffer range, for creating stable organo-mineral exchange sites, to which nutrients can exchangeably attach.

But again, on its own, a lack of nutrient ions in the litter (possibly caused by efficient internal cycling) could lead to the preferential attachment of protons to humic exchange sites and to soil acidification.

The results show such nutrient cycling individualities and give an indication as to the importance of temporal and spatial species diversity within any forest ecosystem.

An interesting aspect with regard to tree species strategies and forest ecosystem dynamics, relates to the postglacial migration patterns of *Acer*, *Tilia* and *Ulmus* spp. in Eurasia and in North America (Delcourt, 1987) and the importance of these species for the creation of fertile soils. These were largely created within the few thousand years between the end of the Pleistocene and the Neolithic times, which

mark the beginning of forest exploitation by introducing domesticated stock and by forest clearing for agricultural purposes.

While species-specific patterns with regard to the synthesis of organic compounds and hence the cycling of nutrients are inherent, differences in amplitude are not only dependent on the composition of the mineral soil substrate, which affects the rate of mineral turn-over of the specific litter (Swift, 1979; Roehrig, 1992), but also species specific.

A differentiation between either, indigenous - or deciduous trees can hence be based on different nuances and intensities with which any of these species influence a particular soil evolutionary trend.

Each region will thus have evolved its own characteristic spatial sequence of species over time, engaged in minimizing entropy by maximising the storage capacity of the ecosystem.

7   Results: Humic fraction elemental contents.

7.1   Elemental contents of humic fractions in percent.

The tables (please refer to Appendix: B.4 *table 2*) indicate that there are structural differences of the humic fractions, which are dependent on the primary resource quality and soil depth. The carbon and nitrogen contents of humic acids vary quite considerably. The elemental percentage difference to 100 %, which is not taken by carbon, nitrogen or hydrogen, consists mainly of oxygen in the form of bridges -O- and active side groups, such as carboxyl, hydroxyl, methoxyl and carbonyl (Stevenson, 1982; Schroeder,1984).

The percentage carbon content of the humic acids is highest at the upper soil level and lowest at the mid soil level under most trees.

The highest humic acid percentage fraction of nitrogen is found under the exotic deciduous trees, slightly less under the indigenous trees and *Eucalyptus regnans* and substantially less under the exotic gymnosperms.

The percentage carbon of the fulvic fraction decreases with depth under exotic gymnosperms and *Eucalyptus regnans* and is generally smaller than the carbon

percentages under <u>indigenous</u> and <u>exotic deciduous trees</u>, except for the upper soil level.

The <u>exotic deciduous trees</u> were found to have the largest sized fulvic acids, containing most of both, carbon and nitrogen, at the lowest soil level. The fulvic acid nitrogen contents measure 2.4% at the upper soil level and increase with soil depth to 3.7% nitrogen content of the fulvic acid. Underneath the other trees the nitrogen contents are decreasing with soil depth.

Molecular percentages of hydrogen in humic acids are generally highest at the deepest soil level under <u>indigenous-, exotic deciduous-</u> and <u>exotic gymnosperm trees</u>. The overall variations are small and are possibly caused by the pH level at the time of freeze drying.

7.1.1   Elemental ratios within the humic fractions.

The elemental ratios are based on the percentages of a particular element with one or the other of the humic fractions.

The C/N ratios of the humic acids are highest at the uppermost soil level under most examined trees, except for *Eucalyptus regnans*, which displays higher ratios at the two lower depths.

The humic acid C/N ratios are lowest under the <u>exotic deciduous trees</u> and under *Plagianthus regius* and *Dacrydium cupressinum*, averaging around 12 and highest under the <u>exotic gymnosperms</u> and in particular *Pinus radiata* and *Eucalyptus regnans*, which display ratios of >20.

The C/N ratios of the fulvic acids exceed the C/N ratios of humic acids under all trees and at all three soil depth levels. The fulvic acid ratios are variable with soil depths and trees. The ratios average at around 20 under most <u>indigenous trees</u>, <u>exotic deciduous trees</u> and *Eucalyptus regnans* and reach between 24 and 41 under the <u>exotic gymnosperm</u> vegetation.

7.1.2   Discussion

The composition of forest humus layers depends on the input of primary (plant residues) and secondary resources (microbial and animal products) and on the decomposition rate of the different compound classes (Swift et al. 1979).

Carbon percentages for the humic fractions have been estimated to range on average up to about 50% for fulvic acids and from 50% to 65% for humic acids, with a corresponding reduction of oxygen percentages from 48% to 40% for fulvic acids and 40% to 28% for humic acids (Stevenson, 1982).

The results of the carbon percentage calculations of the humic fractions are generally in accordance with the published data at the lower soil levels. The carbon content percentages of the upper soil level frequently exceed 65% C for humic acids and at times the 50% C contents for fulvic acids are exceeded. While it can be assumed that the humic structure does contain high amounts of carbon at the upper-most soil level, certain high values can possibly be attributed to inaccuracies of elemental estimations due to high sample ash (NaCl) contents (see 6.2).

However, the data of the elemental analysis gives an indication that there are structural differences of the humic fractions under the influence of various primary producers and at various soil depth levels.

These results are in agreement with many publications (Kononova 1966, Stevenson, 1982, Koegel-Knabner et al 1990).

Changes in the carbon percentage of the humic fractions tend to be mainly associated with soil depth, whereas nitrogen percentage of the humic fractions seems to be related to the vegetation type.

Highest nitrogen contents of the humic fractions are associated with the <u>exotic deciduous</u> and <u>indigenous trees</u> and the lowest with the <u>exotic gymnosperms</u>.

The observed structural differences within and between the humic fractions and the association with biotic and environmental factors have been confirmed by recent research (Rasyid, 1992; Malcolm and McCarthy, 1991).

Malcolm and McCarthy state that: "Each humic component in each environment possesses an individuality that distinguishes it from other components in the same environment, and from the 'same' component in different environments." There are compositional differences among each of the humic fractions from different environments.

"These compositional differences may result in sufficient changes in the chemical, hydrological, or geochemical reactivity of the humic substances that each component should be designated as to the environment from which it was isolated. It is concluded that each humic component in each environment is unique and possesses

an individuality that is characteristic of the particular component and of the particular environment."

The C/N ratios of humic acids and fulvic acids demonstrate that nitrogen is mainly allocated to humic acids and that the litter quality of mainly <u>deciduous trees</u> encourages the formation of humic matter with a low C/N ratio, partly due to the incorporation of bacterial amino sugars (Koegel-Knabner et al, 1990).

Such a ratio is indicative of a net nitrogen mineralization in the soil, which would facilitate protein synthesis and nourish the association of soil biota and with it enhance the process of nutrient cycling, nutrient storage and the nutrient exchange capabilities of the mineral soil.

Valuable research on the structure of humic fractions from forests and the humus types mull, moder and mor was published in various publications by (Koegel-Knabner et al. 1988 to 1992).

7.2   Absolute elemental amounts, allocated to the humic fractions.

The absolute amounts of carbon and nitrogen that are associated with either humic fraction under various primary producers is highly variable. **Absolute elemental allocations** of both carbon and nitrogen with the **humic acid fraction** are on average decreasing with depth under the indigenous trees, exotic gymnosperm trees and *Eucalyptus regnans*.

The exotic deciduous trees, however, show highest carbon and nitrogen allocations with humic acids at the lower and mid soil depth levels.

For the **fulvic acids** the elemental allocations are frequently opposite, in that highest amounts are found generally at the upper soil level. Under the exotic deciduous trees high nitrogen allocations also occur at the lowest soil depth level.

The carbon and nitrogen allocations with **humins** generally decrease with soil depth, except for nitrogen-humin allocations under exotic gymnosperms, which increase with soil depth levels.

Variations of the combined humin and carbonate fractions between samples and between soil strata range from 0.03% C to 20 % C and from 0.001 % N to 0.54 % N.

Notable differences of elemental allocations with humic fractions can be observed. Highest allocations of both carbon and nitrogen are found at all soil depths and for all humic fractions under indigenous trees, closely followed by exotic deciduous angiosperm trees, which both are quite distinct from *Eucalyptus regnans* and the exotic gymnosperms.

Humic acid hydrogen allocations are highest under indigenous and exotic deciduous trees at the mid soil level. For the exotic gymnosperms and *Eucalyptus regnans* the hydrogen allocations of the humic acid fraction decrease with depth and are suB.S.tanially less than for the indigenous- and exotic deciduous trees.

Hydrogen allocations with fulvic acids decrease with soil depth under all trees, but the overall amounts vary significantly. The highest amounts of fulvic acid hydrogen are associated with the indigenous trees, while the lowest are associated with the

exotic gymnosperms, which is a reflection of the observed differences of the exchange capacity.

7.2.1 Elemental allocations to the humic extracts, expressed as percentages of total.

Percentage allocation refers to the allocation of an element to one particular humic fraction, as a percentage of the total elemental amount. Since the percentage allocations of elements are based on averages, an addition of humic fraction percentages does not necessarily add up to 100 %.

Contrary to the absolute elemental allocation, the percentage allocation of carbon with **humic acids** *increases* with soil depth under both indigenous and exotic deciduous trees from 30% to 49 % and 53 % respectively, whereas it remains constant at a low 30 % for all soil depths under the exotic gymnosperms and the eucalypts.

Percentage allocations for nitrogen to humic acids range from 76 % to 84 % under the indigenous trees and from 42 % to 77% under the exotic deciduous trees, with the highest average percentage allocation under both forests at the mid soil level.

Nitrogen allocations to humic acids under the exotic gymnosperms decrease with soil depth from 75 % to 56 %.

Elemental allocations on a percentage basis for the **fulvic acid fraction** are fairly even. Allocations for carbon with fulvic acid are discussed below. Nitrogen allocations are well matched at 11 % to 15 % (8 - 15% for carbon) under the indigenous trees and 7 % to 14 % (8 - 14 % for carbon) under the exotic deciduous trees, increasing with soil depth. Nitrogen allocations to fulvic acids under the exotic gymnosperms measured 16 % (21 % under eucalypt) at the upper soil level. Fulvic acid nitrogen contents were too low at the lower soil levels.

Carbon percentage allocations to **the humin fraction** are high under the indigenous trees at the lower soil depth levels with 83% to 70 %. This is not matched by nitrogen allocations, which decrease with soil depth from 36 % to 28 %.

Elemental allocations to humins under the <u>exotic deciduous trees</u> decrease for carbon with soil depth from 74 % to 38 % (lowest at mid soil level).

However the nitrogen allocations to humins under the <u>exotic deciduous trees</u> match very well the carbon allocations at the three soil depth levels with a range of 69 % to 33 %.

The carbon percentage allocation to humins under the <u>exotic gymnosperms</u> decreases from 50 % at the upper soil level to 4 % at the lowest soil depth. Under the eucalypt the percentage decreases with soil depth from 72 % to 24 %.

The humin nitrogen allocations under the <u>exotic gymnosperms</u> are extremely low at the upper soil level with 3 % (5 % for the eucalypt) and increase with soil depth to 25 %.

Under the <u>indigenous trees</u> the percentage of **hydrogen** of the fulvic acid fraction compared to the humic acid fraction amounts to 32 % at the upper soil level and decreases to 24 % at the lower levels.

Under the <u>exotic deciduous trees</u> the hydrogen percentage of the fulvic acid fraction decreases from 28 % to 21 % with soil depth of the hydrogen amounts of the respective humic fractions.

The <u>eucalypt</u> demonstrates a decrease with soil depth from 36 % to 16 %.

Under the <u>exotic gymnosperms</u> this percentage increases with soil depth from 20 % at the upper and mid soil depth to 43 % at the lowest soil depth level.

7.2.2 Elemental allocations expressed as humic to fulvic acid ratios.

The humic- to fulvic acid ratios of the elements carbon and nitrogen give some indication as to the allocation of elements to one or the other humic fraction. Smallest between group variations of the ratio are observed at the upper soil level, where on average 4 carbon atoms are allocated to humic acids and 1 carbon atom is allocated to fulvic acids.

Under the <u>exotic gymnosperms</u> the highest ratios are found at the upper most soil level and decrease with soil depth.

i.e. The allocation of carbon to fulvic acids increases with soil depth under <u>exotic gymnosperms</u>.

A different trend can be observed under <u>exotic deciduous trees</u> and <u>indigenous trees</u>. The humic to fulvic acid ratios of both carbon and nitrogen frequently increase with soil depth levels.

Increasing amounts of both elements are allocated to humic acids at the lower soil levels.

Eucalyptus regnans displays highest carbon associations with humic acids at the mid soil depth level.

Comparable data were published by Kononova (1966).

7.2.3 Discussion

Elemental allocations to one or the other humic fraction and to soil biota are quite variable.

<u>The influence of indigenous</u> and <u>deciduous trees</u> leads to far higher elemental allocations (C;N;H) at all soil depth levels to the humic fractions and to the fraction, composed of humin and soil biota, when compared to the <u>exotic gymnosperms</u> and *Eucalyptus regnans*.

Koegel-Knabner et al. (1990) suggest that the yields of the humic acid fraction increase with increasing humification of forest soils.

"Humic acids comprise about 25% of the total carbon in the litter layers, but 30 - 60 % in the A horizons.

The yields of the fulvic acid fraction also increase from about 5 % in the litter layer to 15 % in the mineral soils."

The results of this research demonstrate similar average percentages (see 7.2.1).

Under the <u>exotic deciduous trees</u> the carbon percentage allocations for humic acids increase from 30 % to 53 % with mineral soil depth and from 30 to 49 % under the <u>indigenous trees</u>.

However, under the <u>exotic gymnosperms</u> and the <u>eucalypts</u> the carbon percentage allocations for humic acids range around 30 % at all soil depth levels.

The carbon percentage allocations for fulvic acids increase from 7 % to 22 % under the <u>exotic gymnosperms</u> and increase slightly from 8 % to 14 % under the <u>exotic deciduous trees</u> and remain nearly constant at 8 % to 15 % for various soil depth

levels under the <u>indigenous trees</u>, and are a constant 10 % to 11 % under the <u>eucalypt</u>.

The humic to fulvic acid ratios for the elements carbon and nitrogen indicate that under the <u>exotic gymnosperms</u> and with soil depth, the elemental allocations to fulvic acids increase.

This suggest that pyrophanerophytes encourage the preferential synthesis of small and mobile organic acids. These support a translocation of hydrogen ions to lower soil depths, which advances the decomposition of clay minerals, thereby increasing the availability of nutrient ions to pyrophanerophytes. This observation supports H_A 3 A and H_A 15; 16.

The reverse trend can be observed under <u>exotic deciduous</u> and <u>indigenous trees</u>, where carbon and nitrogen is increasingly allocated to humic acids at the lower soil depth levels.

This leads to increases in the exchange capacity for nutrients in the soil and supports the H_A 3 B; 4 A; 6; 7; 9 and 12. The influence of indigenous and exotic deciduous trees is characterized by interactions that encourage nutrient cycling and lead to nutrient storage increases in the organic-mineral soil horizon.

Hydrogen allocations to the humic fractions vary in total amounts under trees and with soil depth and indicate that there are structural and compositional differences in the humic fractions. As stated previously these measurements are to some extent dependent on the pH of the solution at the time of freeze drying. Stevenson (1982) states that the C.E.C. of the humic fractions increases markedly with increasing pH. Furthermore that, in the natural soil, the C.E.C. of the humic fractions and clay can not be considered additive for reasons that some sites are lost through associations between the two. Also many of the organic sites may be tied up as complexes with polyvalent cations.

The nature of the humic fractions and their role in the environment will be discussed in detail in chapter 8, sections 1 and 2.

8 Comprehensive Discussion.

8.1 The Humic Substances.

The results of this research provide evidence for the importance of the litter quality of the primary producers with respect to the structural genesis of -, and the elemental allocation between various humic fractions.

This in turn has direct consequences for the evolution of any soil with regard to nutrient storage capacity.

Malcolm and McCarthy (1991) concluded that there are compositional differences among humic acids from different environments that may result in sufficient changes in chemical, hydrological, or geochemical reactivity that each component could be designated as to the environment from which it was isolated. The same applies to fulvic acids, derived from various environments (soils, soil interstidal water, groundwater, streams, seawater).

Research by Kononova et al. (1966) contributed important aspects on structural variations of humic substances in relation to the involvement of primary producers and associated micro-organisms in various climatically and geologically defined bioregions.

With regard to the formation of humic substances, Kononova suggests that microbial activity, particularly bacterial exo-enzymes constitute the most important factor in humus formation. Most favourable conditions for humus accumulation are achieved when a rhythmical combination of factors allows intense microbiological activity, when new humus substances are formed, and a subsequent depression, which inhibits the decomposition of humic substances. During the periods of microbial depression (caused by soil moisture deficiencies in summer or cold in winter) newly formed humus substances undergo complexation with the mineral part of the soil and are therefore less available to micro-organisms during the subsequent periods of increased activity.

Kononova's suggestions that seasonal changes are the cause of humic acid variations through the year are supported by Andreux et al. (1990), who measured the decrease of humic acids in cultivated soils. Humified compounds accumulate in the upper horizon under deciduous trees from the end of autumn and migrate downwards with the spring thaw. Polymerization and depolymerization processes occur concurrently, the latter gaining dominance during a long humid season.

Actinomycetes and filamentous fungi were found to be mostly responsible for the degradation of polymeric nuclei, whereas most bacteria preferentially utilize aliphatic moieties in humic substances (Toutain, 1981).

Kontchou, (1990) found that humic substances of various origins are very resistant under aerobic and anaerobic conditions against decomposition by mixed bacterial cultures. Swift et al, (1987) provide further information on bacterial interaction with humic substances.

Kononova (1966) discussed wide structural variabilities of the humic substances. The humic acids of boreal conifer podzolic soils are closer to fulvic acids than to the humic acids of other soils. They are highly dispersed, have a high mobility and inferior qualities as structure forming agents, due to a low ratio of aromatic to aliphatic structures in the molecule, which, together with atomic groups in side radicals, determines the predominantly hydrophilic properties of the podzol humic molecule. An acid reaction, excess moisture and weak microbial activity suspend the formation of humic substances at the stage of fulvic acids and fulvic acid like humic substances.

On passing towards the soils of the mixed conifer-deciduous forests to the deciduous forest soil and the chernozem steppe soil the humic acids increase in complexity, loose mobility and acquire the capacity for forming insoluble humates (Ca) and other stable forms of organo-mineral compounds. Associated with this is their increased participation in soil structure formation (soil aggregates of granular structure) and their capacity for accumulation in the soil. The main factors favouring the formation of these complex humic acids are a moderate moisture regime, a neutral reaction and a fairly intense microbial activity.

The pH dependent adsorption behaviour of humic and fulvic acids by montmorillonite, kaolinite, and mordenite is closely related to the adsorption behaviour by Si and Al oxides (Schulthess, 1991). The results showed a strong adsorption of the organics by the Al sites on the Al oxide and kaolinite, and a weak adsorption of organics by the Si sites on the Si oxide, mordenite and montmorillonite. Multivalent cations will form organo-metallic complexes that significantly increase adsorption, particularly on Si sites (Schulthess, 1991).

Research conducted by Ghosh and Schnitzer (Stevenson, 1982) indicates that both humic and fulvic acids behave like rigid spherocolloids at high sample

concentrations and low pH. At low sample concentrations, neutral pH, or low ionic strengths they behave like flexible linear colloids.

This indicates that, in addition to the observed structural differences, and differences in elemental allocations, humic fractions are also responsive to pH changes, in as much as an acidic environment decreases the surface area of a humic substance and thereby the exchange capacity and a neutral pH environment will have the opposite effect (Malcolm, McCarthy, 1991; Stevenson, 1982).

Recent research by Koegel- Knabner et al. (1988 - 1992) and Hempfling (1989) focusses on the identification of structural compounds within humic substances derived from the three forest soil humus types (mull from *Fraxinus* litter, moder from *Fagus* litter and mor form *Picea* litter) and from various soil depths with new analytical techniques, such as cross-polarization magic angle spinning (CPMAS) ^{13}C nuclear magnetic resonance (NMR) spectroscopy and CuO-oxidation.

The results indicate that the major constituents of the fulvic acid fractions are polysaccharides and small amounts of aryl C, irrespective of the soil horizon and that these are derived from water soluble, decomposing plant polysaccharide fractions of the organic layers.

The humin fractions contain high amounts of only slightly altered, plant-derived polysaccharides and lignin.

Only slight changes were recorded for humin and fulvic acids during litter decomposition.

Rasyid et al. (1991) report the major differences between fulvic acids and humic acids to be the increased carboxyl and decreased alkyl C and aliphatic groups in the fulvic acids and that compositions of humic acids reflect their depositional environment.

According to Koegel-Knabner et al. (1988-92):

The humic acid fraction contains less polysaccharides, but high amounts of alkyl carbon and aromatic structures.

The aromatic carbon content remains constant with increasing soil depth.

The moder humus type under beech revealed increasing amounts of aliphatic constituents with soil depth, whereas the humic acid fraction of the mor type under spruce showed higher aromaticities with depth (Koegel-Knabner, 1991).

The three forest humus types under investigation resulted from different rates of litter decomposition, but the decomposition processes are similar. These are characterized by a rapid decrease of polysaccharides and a decrease of O-alkyl carbon (40 %), an increase of alkyl C (25 to 35 %) and carboxyl carbon (10 %) can be detected with soil depth and decomposition. Furthermore, a loss of methoxyl and phenolic groups is evident, reflecting the amount of oxidative decomposition of lignin (and polysaccharides) and causing the relative enrichment of non-lignin aromatic structures (Koegel-Knabner, 1992).

The distribution of lignin phenols in the humic acid fraction increases form 22% in the mull soil type, to moder (52%), and to mor (98%) (Koegel-Knabner, 1988).

Gymnosperm wood lignin produces mainly vanillyl-type oxidation products and angiosperm wood produces syringyl units in addition to vanillyl units. High yields of cinnamyl units are characteristic of non woody angiosperm and gymnosperm tissues. (Ertel et al., 1984).

The composition of humic acids in moder and particularly in mull humus profiles demonstrates a considerable input of microbially produced or microbially altered carbohydrates and amino sugars.

These amino sugars are almost exclusively derived from microbial cell walls (Stevenson, 1982). Microbial residues are even more complex in composition than are plant remains. Bacterial cell walls are composed of peptidoglycans, lipids, and lipopolysaccharides, containing a variety of unusual monomers (Rogers et al. 1980). The cell walls of fungi contain chitin, chitosan, cellulose and a variety of non-crystalline polysaccharides.

Koegel-Knabner et al. 1990 state that:

"A high biological activity in soils (bioturbation) in combination with the presence of clay leads to the incorporation of only slightly modified plant materials into soil organic matter. The action of earthworms promotes transformation of plant residues to humic substances and incorporation of organic matter into stable organo mineral complexes (Koegel-Knabner et al. 1992).

This is represented by a low acid to aldehyde ratio in the A - horizon of a mull (0.35) in contrast to moder (0.50) and mor (0.95) humus.

In mineral soils with low biological activity lignin structural units that have undergone strong chemical alteration accumulate, partly due to the precipitation of highly oxidized, water-soluble, polymeric lignin fragments."

According to Kononova (1966), the litter of deciduous trees advances conditions that are favourable for the new formation and fixation of humus substances. "These soils are characterized by:

1) a high humus content of the upper layer (3-10 cm).

2) absolute and relative predominance of humic acids over fulvic acids, the humic acid to fulvic acid ratio being greater than unity in the upper horizons and greater than 2 in the lower horizons.

The stability of the humus was especially noticable. A large portion of the humic acid is in combination with Ca^{2+} and Mg^{2+}, see also (Stevenson, 1981). Mobile humic acids constitute only 33 % in the upper 10 cm of the soil and 18 % at soil depth of 12 to 19 cm."

Structural differences have been observed not only between soil-vegetation types, with humic acids derived from deciduous forests having a higher extinction coefficient, but also within soil vegetation types. The optical density of humic acids is higher in the lower soil horizons, compared to humic acids from the upper soil horizons under deciduous forests.

The same observations with regard to humus formation under deciduous forests were made in the European part of Russia, Siberia and in the Far East.

This thorough and "down to earth" (Kononova, 1966) research explains well the factors involved in the formation of soil humus substances and, in conjunction with latest compositional research, (Koegel-Knabner, 1988-92) helps to put the results of this research in perspective.

The emphasis is placed on (in that order) plant cover and activity of micro-organisms, hydrothermal conditions, chemical and physicochemical soil properties, and parent rock.

In many soil interpretations this order is reversed, which, based on the conception of geological time frames for soil formation processes, advances the illusion that soils possess an immunity against exploitation and mismanagement. Soil degeneration is however an incredibly fast process. Soil degeneration has historically and repeatedly been the cause of cultural decline and is nowadays taking place on a world wide scale.

Kononova highlights the importance of studying the pattern of the processes by which organic matter is accumulated and decomposed under different soil management regimes. In all Russian biomes the humus content decreases drastically with the ploughing-up of virgin lands and with the long term continuous cultivation of annual crops, due to an insufficient formation of new organic substances.

Andreux et al.(1990) found that the complete removal of (tropical) natural forest leads to a considerable loss of humic acids and increases of fulvic acids, correlated with a decrease of soil structure and porosity and an increase of soil bulk density, followed by a dramatic reduction of crop yields.

Contrary to traditional western approaches of NPK fertilization, which do not address the main problem of S.O.M. loss, Kononova suggests that a systematic fertilization with farmyard manure is one of the measures favouring soil improvement. However only one third to one fourth of the total manure applied increased the soil humus, the majority being mineralized. In addition farmyard manure has a weak effect in restoring soil structure.

The temperate forest deciduous trees and the New Zealand indigenous trees are able to remedy this problem.

8.2 Ecosystem Responses to Management.

Ulrich (1987) warns that there are reasons to be concerned about the stability of the ecosphere and suggests that the **destabilizing changes** have one common denominator: "They can all be expressed as **storage changes** (of species, of nutrients, of chemical compounds, of acids and bases, of organic matter) and thus reflect changes in the balance of matter in the ecosphere.

Stable ecosystems are characterized by a matter cycle, which is in a quasi steady state and governed by the principle of self-organization, which is based on a tendency to minimize entropy production."

Managed forest ecosystems, from which biomass is exported deviate usually further from the quasi steady state than the natural forest ecosystem.

From a theoretical point of view managed forest ecosystems can reach stability phases if the deviation from steady state remains within the range of elasticity. Elasticity can be expressed as the change in capacity which the ecosystem can suffer without being subjected to a long-term change in species composition and in storages (Ulrich, 1987).

Unequal rates of formation and mineralization of organic matter and of the exchange of matter between the ecosystem and its environment are the consequence of a de-coupling of processes.

The results of the thesis demonstrate the presence of de-coupling processes that are associated with the nutrient extraction strategies of pyrophanerophytes (see 6.2.2.; Pryor, 1976, Marschner, 1986, Leyval, 1990).

The influence of pyrophaneropytes causes a depletion of organic matter storage in the mineral soil. This storage decrease leads to a reduction of the CEC. The humus disintegration is characterized by uptake or leaching of nitrate, which leads to a strong soil acidification, concerning all horizons in which organic matter was accumulated (Ulrich, 1987). The loss of SOM reflects an increase of entropy due to the loss of chemically bound energy.

A further de-coupling process is associated with pyrophanerophytes and relates to the spatial and temporal divergence of ion uptake and ion release.

The process starts if nitrification is inhibited in the organic top layer, which is characteristic for raw humus (Baum, 1975).

The acidification is advanced by the spatial de-coupling of ammonification and nitrogen uptake (Ulrich, 1987).

An additional cause of acidification relates to the application of N as artificial fertilizers. In this case, the net proton production in soils corresponds to the cation excess in the formed biomass. If the total increment is harvested and exported, the soil acidification caused in this way remains.

In contrast, the natural N accumulation in biomass is not connected with a net proton increase (Hauter and Steffens 1985).

Hence, the rate of accumulation of soil organic matter should depend upon the rate of nitrogen fixing, since nitrogen is an integral part of the organic matter accumulated and must come into the ecosystem mainly from N_2.

8.2.1 The soil buffer ranges.

8.2.1.1. Generative conditions.

The results demonstrate that the litter of exotic deciduous angiosperms and indigenous trees advance a soil reaction that leads to the dominance of the silicate buffer range.

In the silicate buffer range (dominance range between $6.2 > pH > 5$) the kinetically stable acid neutralization capacity of the primary silicates is transferred into the kinetically labile, mobilizable acid neutralization capacity of the weathered clay minerals with a permanent negative charge. The exchangeably bound nutrient increase, results in an increasing elasticity of the ecosystem.

The mull humus type is associate with soils in the silicate buffer range and the carbonate buffer range ($8.6 > pH > 6.2$) and with ecosystems in the aggradation phase or in the stability range with high elasticity.

Since acid tolerance is of no importance in competition, a great diversity of species and the activity of earthworms ensures the accumulation of organic matter throughout the whole rooting zone.

8.2.1.2. Degenerative conditions.

Conversely, the results demonstrate, in agreement with research of other authors (Ulrich, 1987, Walter, 1985-87), that the pyrophanerophytes promote de-coupling processes that lead to a rapid degeneration of the ecosystem elasticity from the exchanger buffer range ($5 > pH > 4.2$) into the aluminium buffer range ($4.2 > pH$) and under some individuals the aluminium / iron buffer range ($3.8 > pH$) is reached. In the exchanger buffer range, at pH levels of < 5, the main reaction products of silicate weathering are either nonexchangeable polymeric Al-hydroxo-cations, leading to a reduction of the CEC, or Al^{3+} ions, leading to a reduction of the base saturation. At a base saturation of < 15 %, Al ions appear in the soil solution

and acid toxicity commences (Marschner, 1986). This threshold has been surpassed under the influence of most pyrophanerophytes of this research.

In the aluminium buffer range (4.2 > pH) Al^{3+} may become the dominating cation in the soil solution and at pH levels of < 3.8 Fe oxides are included in the buffer reactions in the presence of dissolved organic matter.

The described pyrophanerophyte characteristics lead to a rapid podzolization of the substrate, which if uncontrolled, will deteriorate to a vegetation type called an "**acid steppe**", characterized by heathland on sandy soils and acid tolerant grasses on soils with higher silt and clay contents.

Podzolization played a large role in Northern, Northwest, and Central Europe as a consequence of anthropogenic misuse of forest ecosystems; almost all podzols existing in these areas are man-made (Ulrich, 1987).

Natural podzolization occurs at the treelines, in the boreal zone and in high rainfall areas of the west coast of New Zealand and is primarily climatically determined. Podzolization processes under Kauri forest association result from both, Kauri litter and the age of the soil and plant association.

The Kauri forest association can be described as experiencing an edaphic climax (Jenny, 1983). The kaolinite clay fraction of the mineral substrate is rather high and few minerals are left to weather. Eventually geological processes will end edaphical climaxes and allow for a new enduring ecosystem to evolve with new weatherable minerals and increasing amounts of soil organic matter.

8.2.1.3. Restorative conditions.

A reversal of the de-coupling trends depend on the mineral composition, on the reserves of the substrate and on a reduction of the proton load, by the planting of appropriate species.

The mineral reserves will set boundaries as to whether forest ecosystems can eventually reach a stability with low elasticity or with high elasticity.

Soils consisting of quarz and kaolinite or their mixtures can not recover.

Substrates, that contain weatherable minerals however can be redirected with the appropriate planting of mixed forests towards a process of de-acidfication as shown by the results.

The recovery of acidified systems is a very slow process and limited by the supply of nitrogen. There are very few species with an ablility to fix nitrogen under acidic soil conditions.

As explained previously, artificial nitrogen fertilization aggrevates the problem of de-coupling. This means that the base saturation needs to increase to some extend before nitrogen-fixing species can invade and eventually restore a forest ecosystem .

8.3 Nutrient Cycling and Forest Ecosystems.

The responses of the loessial soils to forest clearance and reafforestation have been documented with this research.

Following the complete clearance of the indigenous forest, the loessial soils responded within a few decades, with a rapid loss of organic matter, an increase in bulk density, surface erosion and gleying, (Tomlinson, 1977).

This research documents the soil evolution over 80 to 100 years under the influence of an intercontinental assemblage of trees from the temperate forest biome.

A soil rehabilitation response is evident following re-afforestation with indigenous and exotic deciduous trees.

Yet further soil deterioration is apparent in case of reafforestation with fire trees.

8.3.1   Indigenous forests and the effects of mixed species on forest nutrient cycling.

Fleming (1977) examined the history of life in New Zealand and summarized that New Zealands forests are most like the Mesozoic forests of Gondwanaland. The reason for this is that New Zealand escaped the late Tertiary desiccation, which elsewhere triggered off the evolution of savannas and steppes and led to floral differentiations and to the evolution of fire adapted trees like the eucalypts in Australia. This is the reason why the indigenous vegetation has world heritage status and needs to be part of the development of our national culture, with skylines of native forest in all districts.

The results of my research are complemented by research of Mark and McSweeny (1990). The diversity of **forest-floor invertebrates** of selected indigenous forests and *Pinus radiata* plantation in north Westland was compared (Dugdale 1974). The *Pinus*

radiata plantation featured 60 invertebrate species compared to 170 species in an indigenous forest with *Nothofagus fusca, Dacrydium cupressinum* and *Dacrycarpus dacrydioides* as canopy forming species, and 125 species in an indigenous hillcountry forest of mixed canopy species composition. Even a poorly drained terrace of indigenous gymnosperm forest had 85 species of soil invertebrates. This comparison elucidates that the soil vitality under *Pinus radiata* is lower than that of even the most inhabitable indigenous forest soil.

The nutrient content of the above ground biomass and the litter of a podocarp-hardwood forest in Westland was analysed (Levett, et al., 1985). The rationale for this research was to establish the amount of nutrient removal from the forest ecosystem under chipwood logging extractions.

Indigenous **canopy trees** seemed to contain higher amounts of nutrients in the green foliage compared to **understorey trees**, and the latter had higher nutrient contents in branches and stems of > 1cm, when compared to the canopy species.

Litter decomposition rates of common indigenous trees in a *Agathis australis* forest are shown by Enright and Ogden, (1987). "In general, broadleaf mesophyll species litter is more nutrient rich than either gymnosperm or broadleaf sclerophyll species litter. Senescent leaves of *Melicytus ramiflorus* have particularly high concentrations of potassium, calcium and magnesium.

High concentrations of calcium, magnesium and phosphorus were found in the leaves of *Melicytus ramiflorus, Ripogonum scandens, Pseudopanax arboreus, Elaeocarpus dentatus,Beilschmiedia tawa*, which favours rapid decomposition. There is a clear relationship between litter type and rate of nutrient loss with mesophyllous species loosing nutrients more rapidly than sclerophyllous species. The broadleaf sclerophyllous species *Knightia excelsa*, the gymnosperms *Agathis australis, Phyllocladus trichomanoides* and the fern, *Dicksonia squarrosa* shed litter with low concentrations of nutrients, that resist decomposition. "The importance of each species and litter fraction to the cycling of nutrients in the kauri forest ecosystem depends both upon the rate of release of the elements during decomposition, and the absolute amounts added to the forest litter store by litterfall. It is likely that as biomass of kauri in a stand increases, the rate of cycling of nutrients declines."

The importance of species diversity for the nutrient cycling processes has been illustrated by research conducted by Lambert and Turner (1986) in a New South Wales sub-tropical rainforest.

"All nutrients analysed varied between species. Some individuals accumulated high concentrations of specific nutrients, but an accumulator of one nutrient was not necessarily an accumulator of any other.

There are similarities within families and within genera for specific nutrients.

Assessment of nutrient concentration on the basis of forest strata showed major differences. The large shrub stratum had the highest concentrations of N, P, K and B. The mean concentrations of Al, Na and Cl were highest in the small shrub stratum, mainly because several species accumulate these elements.

Nurients were accumulated in higher concentrations on a disturbed site than on an undisturbed site. This has been discussed in relation to nutrient conservation mechanisms after disturbance."

These results provide prove for the importance of species diversity for the best possible site utilization.

Additional information on the dynamics of indigenous forests is summarized in the appendix.

8.3.2. Deciduous trees.

The spatial patterns of trees in natural forests of East-Central Europe was examined by Szwagrzyk (1993). The trees included *Abies alba, Acer campestre, Acer pseudoplatanus, Carpinus betulus, Fagus sylvativa, Fraxinus angustifolia, Picea abies, Tilia cordata* and *Ulmus glabra*. "The general pattern of tree distribution was overwhelmingly random. Fine scale patterns (with distances among trees not exceeding 15 m) were usually intermediate between random and regular. The widespread opinion that competition among trees leads to regular distribution of canopy trees in mature climax forest stands could be maintained only in its less rigorous version. The lack of significant trends towards negative or positive associations between different tree species suggests that there are no direct influences (such as allelopathy) which are essential in shaping spatial relationships

among tree species. There was no significant spatial relationship between the distribution of large and smaller trees. However the overwhelming dominance of random to near-to-random spatial patterns does not necessarily mean that processes operating on tree populations are truly stochastic; they may be non-random without tree distribution showing this."

The research objectives and the results of Weber et al. (1993) correspond in several aspects with the results of my research.

Weber et al. (1993) analysed the effects of the re-introduction of deciduous trees to a plantation monoculture of *Picea abies*. Historically, the economic doctrine of rapid production and rotation monoculture management was responsible for the replacement of the original forest of mixed deciduous trees with the monoculture plantation of *Picea abies*. The soil pH levels decreased significantly and a rapid podzolisation of the loess soil had established. The realization that the *Picea abies* monoculture was responsible for a rapid degeneration, particularly of weakly buffered soils, led to the stepwise re-introduction of the deciduous trees *Acer pseudoplatanus*, *Fagus sylvatica* and the conifer *Abies alba* since 1942. Tree induced changes to the nutrient contents of the mineral soil were analysed. The soils under deciduous trees consorted with the mull humus type, indicated by an intensive bioturbation and associated with increases of C in the mineral soil and N in association with humus mineral complexes, as well as considerable increases of mineral cations. The mineralization of the latter from the organic layer caused an increase of the pH and the soil buffer capacity with the complexation of base cations with the soil humic material. The base saturation increased accordingly. The soil contents of exchangeable manganese and iron remained the same for soils under *Picea abies* and the mixed forest. The increase of the base saturation in the mixed forest was attributed to an increase of the CEC on humic material and a preferential storage of cycled calcium and magnesium at the new exchange sites. The positive influences of the mixed species forest was most pronounced after 45 years. Positive tendencies were recognizable after 15 years. Additional positive effects resulted from the height differences of the admixed trees. These included an even moist climate, a rapid warming of the soil underneath the leafless deciduous trees in early spring, which encourages the decomposition processes and the activity of soil organisms. The mixed age-species forest contributes thus to a balanced and continuous cycling of nutrients.

The influence of different forest types on the soil development was examined by Kundler (1962). Whether a mull or mor humus generating association of decomposing organisms inhabit a particular site depends on 1) quality of plant litter and 2) soil type. The quality of plant litter depends on the species specific 1) amount of nitrogen 2) contents of mineral nutrients and bases 3) contents of phenolic and chinoid combinations.

The C/N ratio of the litter of various deciduous shrubs and trees, from the same location was measured by Wittich (1961) with the following results:

Sambucus nigra 12 ; *Alnus glutinosa* 16; *Alnus incana* 19; *Ulmus montana* 23; *Fraxinus excelsior* 24; *Ulmus laevis* 24; *Ulmus campestris* 25; *Carpinus betulus* 27; *Corylus avellana* 28; *Prunus padus* 31; *Salix caprea* 37; *Tilia europaea* 37; *Betula pendula* 45; *Picea abies* 48; *Acer pseudoplatanus* 51; *Sorbus aucuparia* 54; *Acer platanoides* 56; *Pinus nigra* 65; *Thuja plicata* 67; *Pseudotsuga menziesii* 77; *Larix decidua* 77.

The litter contents of acids and bases were expressed as a ratio for the following trees: *Fraxinus excelsior* 1.06; *Ulmus glabra* 1.1;   *Acer platanoides* 1.26; *Fagus sylvatica* 1.35; *Quercus robur* 1.47; *Picea abies* 1.68; *Pinus silvestris* 1.74.

Kundler suggested that the mineral availability of the substrate also helps to maintain a soil humus type. A mineral rich sub-soil was found to yield litter, richer in mineral content and also supported a ground flora with favourable nutrient contents.

The mor humus type generates copious amounts of fulvic acids, which leach to lower horizons and are thought to be responsible for the leaching of minerals and the degeneration of soils to podzols. In conclusion Kundler summarizes: "Where soils are labile a change of stocking can have distinct consequences on the soil development. We must take it our object to stimulate the formation of the mull humus type and the development of deep going intensive root formations on as many forest soils as possible by means of site preparation fertilizing and choice of species."

The effects of angiosperm litter in conifer forest was compared with the artificial fertilization of conifer forest by Mettin (1986). Comparisons were completed for two associations: 1) *Picea abies* and *Fagus sylvatica* and 2) *Pinus silvestris* and *Tilia europaea*. Mettin cites Schmidt, who detected that the artificial fertilization of pine forest with N, P_2O_5, K_2O and CaO resulted in smaller increments when compared to the increments of pine, benefitting from litter inputs of admixed *Tilia europaea* trees. The

increment of pines in association with *Tilia europaea* increased with age (up to 10 years = 106%; up to 20 years = 117%). Mettin reached the conclusion that conifers tremendously benefit from the association with angiosperms and relates the increments of conifers to the angiosperm related maintenance of a beneficial soil humus type, associated increases of the pH, nutrient availability, and a general increase of the humus mineral horizon. He recommends therefore that an admixture of 30 to 40 % of angiosperms is indispensable and that the positive effect will be increased the higher the percentage of angiosperms in the forest.

Gayler (1985) discusses the economic gains achieved in forestry enterprises, following the admixture of angiosperms to conifer plantations. The forestry district Erdmannshausen began admixing angiosperm trees to a pine monoculture in 1895. The beneficial effect of the angiosperms increased the stock from 117 Vfm/ha (Festmeter {m^3} by volume) in 1896 to 193 VFm/ha in 1966 and to 213 VFm/ha in 1972. The harvestable timber volume increased from 2 Efm/ha in 1887 (extractable Festmeter) to 4 Efm/ha in 1926 and to 5.3 Efm/ha in 1966. In another forestry district the amount of harvestable timber increased following the admixture of leaftrees to pine forest from 2 Vfm/ha/a in 1913 to 4.6 Vfm/ha/a in 1966. Other benefits of the admixture of oaks and beech to a fir forest include reduced risks of damage to young firtrees by ungulates, due to ample food resources in form of oak and beech seeds during winter.

Different species specific nutrient releases during litter decomposition were examined by Blair (1988). Litter of three species decomposed in the following order (fastest to slowest): *Cornus florida* > *Acer rubrum* > *Quercus prinus*. There was an indication of greater increases in N, S and P concentrations per unit mass lost in faster decomposing litter types. N release began when the C/N ratios decreased to between 25 and 34. Patterns of P and S fluxes varied more among litter types. Only *Cornus florida* appeared to release P by the end of the study and an immediate release of S which continued throughout the study. The other litter types immobilized S.

These examples give evidence as to the importance of the mixed species composition of forests and the individual contribution of each species to the genesis of the soil solution.

The fluxes of organic nutrients and humic substances in a deciduous forest were examined by Quallis et al. (1991). The mixed species forest was composed of *Quercus* spp., *Carya* spp., *Acer rubrum*, *Nyssa sylvatica*, *Cornus florida*, *Fraxinus* sp., and *Fagus sylvatica*. In throughfall, about half of the dissolved N and P was organic. In solution from the forest floor, 94% of the N and 64% of the P was organic. While most of the inorganic N and P were removed by microbial immobilization, the substantial input of humic substances made an important contribution to the humic N absorbed to the mineral soil.

In agreement with my suggestions, Muys and Lust (1992) found that the dominant tree species is more important in determining the biological and chemical fertility of the stand than the soil texture and the climate.

Once soils were degraded, it was found that neither a change of tree species nor liming were wholly successful in soil reactivation. The authors appeal for a global strategy to rehabilitate degraded loams, based on integrating the choice of tree species and rectifying the nutrient inputs in conjunction with the introduction of earthworms.

A second study by Muys et al. (1992) investigated the ecological effects of grassland afforestation. Different tree species were found to be responsible for differences in the mineral A horizon. Litter of *Prunus avium* and *Tilia platyphyllos*, *Alnus glutinosa* and *Fraxinus excelsior* was found to be very fast to decompose, and would lead to the formation of a mull humus type. Earthworms were principally responsible for the litter decomposition of *Prunus avium* and *Tilia platyphyllos*, whereas the high decomposability of *Alnus glutinosa* and *Fraxinus excelsior* litter ensured a mull humus type, even with low populations of earthworms. The *Quercus palustris* litter with a ratio C/N >32 started to accumulate and led to the formation of a moder humus type.

In conclusion, mixtures of different litter qualities should be researched and limits determined from which litter starts accumulating. The maintenance of a mull humus type should be encouraged by the choice of tree species. This will be advantageous for the creation of a stable and diverse forest and is a necessity in case a future conversion to agriculture is required.

Klemmendson (1991) examined the Oak (*Quercus gamelii*) influence on the nutrient availability in Pine forests (*Pinus ponderosa*) of central Arizona. The research results

showed that the oak is an efficient absorber and accumulator of nutrients, in line with the expected effect of most broad-leaved species. "The concentration of each of seven elements was much greater in oak leaves than in pine needles, collected from trees growing side by side in the same forest stand." "Klemmendson (1987) showed that the concentration of most nutrients increased in the forest floor and upper soil layers of pine-oak stands as the amount of oak increased from 0 - 70% of total basal area."

Gatto and Rinaldi (1986) examined possible responses of exploited forest systems and tested mechanisms for a catastrophic system collapse. It is based on a model of the dynamics of forest biomass and soil nutrients and on the fact that mortality may become very high when soil acidity exceeds a threshold. The soil acidity may have several causes, one of which is by exogenous fertilization, (Ulrich, 1987). It is shown that an increase of exploitation may give rise to a catastrophic and possibly unexpected collapse of the forest.

Falkengren-Gerup (1993) gathered experimental evidence for the relative sensitivity of deciduous forest plants to high soil acidity. It is suggested that the high acidity of the rhizosphere solution, aggrevated by harmful levels of easily reacting, mainly monomeric Al^{3+}, obstructs the uptake or retention of mineral nutrients by the roots.

8.3.4. Pyrophanerophytes and management.

The population dynamics of the montane conifer forests in the Western Cascade range in Oregon is characterised by regeneration patterns that are strongly influenced by natural disturbances and species' life history. (Stewart, 1986). "Periodic fires of variable intensity and extent have produced a mosaic of relatively even-aged patches of different conifer species. If *Pseudotsuga menziesii* dominated early, regeneration of *Tsuga heterophylla*, and often *Abies amabilis*, was rapid. If, however, *Tsuga heterophylla* established first after fire, further regeneration of other species was absent or minimal until canopy openings formed."

The natural dynamics of pines and eucalypts are explained in the Appendix: A. 2.

The major differences between these pyrophyte ecosystem dynamics and the dynamics of deciduous or indigenous forests are illustrated when the spatial patterns of trees of the North-west American conifer forests is compared with the above description of the spatial analysis of tree distribution by Szwagrzyk, 1993, and with publications of other authors (Walter, 1985-87; Reichle, 1970; Dengler, 1992; Brockie, 1992).

Early concerns about the effects of pine plantations in New Zealand included reports on changes to the original organic matter status, structure and consistence characteristics of some soils (New Zealand Soil Bureau, 1954; Thornton et al.,1956; Bond 1960).

The soil chemical change was determined following a three decade afforestation with pine (*Pinus taeda*) on a previously cultivated Ultisol (Richter et al. 1994). The soil organic matter had been severely depleted during 200 years of shifting and intensive agricultural practices in which wheat, corn and cotton crops were grown. Thus the CEC showed a small increase following the tree plantation. During the pine plantation period the acidification of the soil was most rapid in the upper layers, but extended throughout the upper 0.6 m of soil. The pines caused a depletion of one half of the exchangeable Ca and Mg cations within the upper 0.6 m soil layer. The cation loss was attributed to approximately equivalent rates of cation removal by biomass accumulation and soil leaching. Total K removals from the soil exceeded reductions in soil exchangeable K by nearly 20-fold. The K removal by pines could be compensated for by a combination of large amounts of wheatherable K in the mineral soil and throughfall of leached K.

Richter et al. suggest that "these nutrient dynamics may be common to many nutrient-demanding forest systems, ... and that the rapid decrease in soil Ca and Mg supplies suggests that multiple rotations of productive tree plantations are not sustainable."

Adams (1978) warns that most forest management practices appear to be based on their utility and practicality with little attention given to their impact on the soil. He suggests that the importance of conserving the soil resource in forest management needs particular emphasis in low nutrient forest ecosystems, and foresters should be aware of the increased significance of poor management practices on such soils.

Adams contrasts the ecosystem nutrient dynamics dominated by an organic cycle on the mineral nutrient deficient substrate of the West Coast hill soils, with the mineral rich substrate of the lowland alluvial soils.

He suggests that clearfelling, and associated practices of burning, roading, skidder and hauler logging and windrowing accelerates the rate of ecosystem deterioration.

Adams calculates that, on the nutrient poor soil, a hundred year period of conventional pine monoculture management, represents a loss of phosphorus from the system equivalent to that occurring naturally in 20,000 years.

The same 100 year period (three pine rotations) on mineral nutrient rich soil accounts for the removal of total soil phosphorus approximately equivalent to that occurring in 1000 years in a comparable undisturbed ecosystem.

Adams concludes that it is desirable that foresters re-examine their approach to fertilizer application, which has been reactive rather than proactive.

However, as Ulrich's (1987) paper suggests, there is no quick fix to exploitation. Reduced amounts of SOM and the acidification of soil following nitrogen fertilization demonstrates that artificial fertilization will at best temporarily cover up symptoms of decline.

The only permanent solution rests in the re-establishment of the original type of mixed age and species forest cover.

Soil properties as affected by *Pinus radiata* plantations were compared with the soil properties under *Eucalyptus* forest in Australia at two sites with contrasting nutrient status (Turner and Lambert, 1988). At the lower fertility site, the soil under *Pinus radiata* was subject to accelerated nutrient depletion, evidenced by lower soil contents of nitrogen, exchangeable magnesium, and a lower soil pH, and higher amounts of organic matter and exchangeable aluminium than soil under eucalypt forest. At the higher fertility site, the soil under pine had lower concentrations of nitrogen and organic matter than the soil under eucalypt forest.

The soil organic matter content seemed to be the main property influenced by plantation establishment.

A similar research objective compared the effects of *Pinus radiata* plantation and indigenous forest (beech or podocarp) in five widely seperated forest sites in the South Island in New Zealand (Goh and Heng, 1987). "In exotic plantations, the net forest floor accumulation was modified by management practices, such as burning, during the process of <u>converting native forest to pine plantation</u>, and stand thinning."

It is suggested that the nutrient mobilization, following the disruption of the native nutrient storage mechanisms by the above mentioned management practices, is a likely explanation of the results.

In addition, the effects of a first rotation pyrophanerophyte with respect to its nutrient extraction strategies, as discussed in this research would explain some of the unknown factors that are mentioned in the paper and that contribute to the interpretation of results, in regard to

"the superior available nutrient status under pines,"

and the erroneous conclusion that

"topsoils under pines might be thought to have a greater nutritional potential for sustained tree growth than would be the case with those under beech."

A paper discussing the influence of pine forestry on soil Dyck et al. (1985) argues that there is no evidence that soil degradation under radiata pine is inevitable and suggest that managers can rapidly alter site quality.

The argument is discussed, that site productivity is possibly of much greater importance than the important influence of a species on the soil development. The N.Z. Soil Bureau, (1954) published the well known phenomena of the Kauri (*Agathis australis*) "egg cup podzol", demonstrating, in New Zealand the powerful effect of organic parent material on soil development.

This research, that of Lambert and Turner (1986) and Enright and Ogden (1987) indicate that within site and between species variations exceed those of between site and within species variations of nutrient cycling capability and effects on soil nutrient storage. In consequence, the most powerful tool of forest managers is the proper choice of species.

Dyck et al. (1985) suggest that, if the productivity of a pine stand is high, decomposition is rapid and nutrients are available for growth.

This suggestion is correct and incomplete. The productivity is a result of a de-coupling of the decomposition process , which will inevitably lead to site degeneration, caused by the pine species (Ulrich, 1987) and to a scenario of low productivity, with slow decomposition, soil acidification and podzolisation.

The statement that nitrification is a soil acidifying process, , is only correct if it refers to artificial N fertilization, but incorrect, if it refers to the nitrification of in situ ammonia. Ammonia is a product of microbial decomposition and attaches in exchangeable form to clay and humus. There is no net increase of hydrogen into the soil solution, following the nitrification of natural in situ ammonia.

However, the nitrification process of ammonia, applied as fertilizer will lead to soil acidification,by nitrate leaching and with the removal of the biomass (Ulrich, 1987; Jenny, 1983). Hence the argument that soil acidification is proceeding at a much faster rate under gorse and other N-fixing plants than under plantations containing non-N-fixing plants is incorrect, in fact the opposite is true if pine plantations are fertilized.

The reasons for a decline in productivity are not that difficult to determine, as implied by Dyck et al. (1985) These reasons are not primarily based on soil type, climate , genetic changes in planting stock, but are due to the loss of soil organic matter and nutrients in the mineral A horizon, caused by a de-coupling of the decomposition process, induced by pine nutrient extraction strategies and unsuitable establishment practices.

It is suggested that this research elucidates plant strategies and that now, there is reason to understand that both, current management practices and pyrophanerophytes nutrient extraction strategies have a negative effect on almost any site, fertile or infertile.

Changes in the soil under *Pinus radiata* were reported by Hamilton (1965).

Important changes in soil properties were demonstrated under the pines. These include increases in bulk density, colour value, C/N ratio and

decreases in organic matter, C, N, P, exchangeable cations, CEC and moisture holding capacity and strongly suggest declining suitability for plant growth.

In agreement with my suggestions, Hamilton concludes that

> "In growing forest crops, natural fertility levels must be maintained or even
> improved if continued removal of forest produce is to be undertaken. A

steady level of productivity is largely dependent on the repeated use of the nutrient capital through the recycling of elements temporarily synthesized into organic compounds and tissue. Much of this capital has accumulated over a long period of time,"and represents the temporal and spatial succession by a great number of species as a plant-soil ecosystem.

A realization on insufficient research on the effect of introduced plantation species on soil properties encouraged research by Jurgensen et al. 1986, who compared the soil development under *Pinus radiata* and *Eucalyptus regnans* plantations. "The litter decomposition rates were clearly lower under *P.radiata* than under *E. regnans*. Differences in the mineral soil nutrient status had developed by age 4 years with more total nitrogen and exchangeable calcium, but less exchangeable magnesium in the top 40 cm of soil under *E. regnans* than under *P. radiata*."

The results of a second paper by the same authors, Jurgensen et al. (1985) found striking differences among *Pinus radiata*, *Eucalyptus regnans* and *Acacia dealbata* stands. The soil under *A. dealbata* contained over 60 % more nitrogen than *P. radiata* and 40 % more than *E. regnans*. The authors suggest that "the use of a nitrogen-fixing tree such as *Acacia dealbata* could yield considerable amounts of wood and improve soil nitrogen status".

However, while *Acacia dealbata* will improve the soil nitrogen status, a large scale rotation with pines will lead to considerable soil acidification via the biomass export of both species, which induces a de-coupling of the nitrogen cycle (Ulrich, 1987).

Only the insitu decomposition of nitrogen containing compounds of the biomass to NH_3 will increase the soil pH level, by assimilating hydrogen ions out of the soil solution that previously were released into the soil solution by the nitrification process.

An understanding of nutrient cycling processes is essential for any future forest manager, so that the current de-coupling of nutrient cycles and the subsequent destabilization of forest-soil ecosystems can be avoided in future.

As Madgwick (1985) pointed out "There are clear gaps in our knowledge....Until such time as our knowledge of the various factors affecting dry matter production and nutrient cycling is more complete, estimations of dry matter production and

nutrient removal from plantations of *Pinus radiata* grown under any silvicultural regime will be subject to considerable error."

Concerns with *Pinus radiata* plantations in New Zealand were summarised on the 7th North American Forest Soils Conference by Dyck and Skinner (1990).

A second rotation decline in *Pinus radiata* plantations had been detected in Australia (Keeves, 1966) and in the early 1960's on the Moutere gravel soils, predominantly Typic Hapludults, in the Tasman district (Stone and Will, 1965).

The nutrient extraction strategies of pyrophanerophytes, identified in this research, were apparent from reported research (Stone and Will 1965; Will, 1968). The second rotation decline was caused by the feeding of pines and their associated mycorrhizza (Chu-Chou, Grace, 1990), on stored nutrient reserves in soil organic matter, deposited by previous indigenous primary producers.

Actinomycetes and filamentous fungi were found to be mostly responsible for the degradation of polymeric nuclei in humic substances (Toutain, 1981) See section 6.4.1.

A suggested reason (Stone and Will, 1965) for the second rotation decline was that during the first rotation the N, contained in the soil organic matter, was decomposed and was made available to the *Pinus radiata* by the mycorrhizal root system of the pine.

By the second rotation this resource had been exhausted.

This hypothesis was supported by a subsequent investigation on soil bleaching. It was found that bleached zones under *Pinus radiata* contained large amounts of mycorrhizal hyphae and very low levels of nutrients, compared to normal black soil away from pine roots (Will 1968).

Kingston's thesis (1968) examined the soil properties and the root structure that are associated with the regeneration of *Pinus radiata* on depleted soils. The shallowness of the horizontal feeding root system was verified for ridge and gully positions. The gully trees appeared to have a more vigorous vertical root system.

The issue of pine mineralization of soil organic matter is also addressed by research of (Fahey and Knight, 1986).

It seems that the promotional suggestions of the pine industry and the Forest Owners Association on a "conference on sustainable land management in 1991" in Napier New Zealand, with regard to the "beneficial" effects of pine plantations on the reduction of atmospheric CO_2 greenhouse gases are not only incorrect but misleading.

> The effect of pines and other firetrees may in fact lead to a substantial decline of the vast stores of soil carbonaceous material and an associated considerable increase of atmosperic CO_2.

In consequence, pines and other fire trees support the rapid approach of a "point of no return", with regard to a drastic change of the earths climate, as suggested by Hamaker and Weaver (1983). The exhaustion of soil mineral nutrient stores may lead to advances of fire trees and cause the release of organic carbon into the atmosphere, which will end the current inter-glacial, by initiating a greenhouse effect, which may provide the energy required to initiate a glacial period.

Research on the effects on management techniques has since replaced research concerned with the effect of pines on soils.

Despite evidence that clearfelling operations lead to a depletion of soil carbon (Swift, 1979, O'Connell, 1987, Dengler, 1992), through increased rates of microbial mineralization of soil organic matter, this practice continues unabated.

To facilitate planting and to reduce competition, clearfelled areas are usually windrowed (rootraked), even on steep slopes. Windrowing removed more than 10 cm of topsoil at one site, at another site 13 cm of topsoil were removed, containing appr. 2800 kg N/ha, as well as other nutrients.

Nutrient losses due to burning are repoted to be significant for N, K, Na, and Mg (Maggs, 1988).

Baker et al. (1986) found that "despite the large inputs of N in the past the *Pinus radiata* trees in all treatments are currently N-deficient...The highly N-immobilising nature of the ecosystem suggests that continuing N-inputs by either biological N2-fixation or by fertilizer will be necessary to maintain growth rates in the long term." Fertilizer input and long-term pine plantations have since been shown to be unsustainable (Ulrich, 1987).

Trials during the 1980's compared the effects of herbicides, versus rootraking, versus burning as methods of pre-planting site preparation, resulting in the identification of one method being slightly less of a blunder, compared to another. The continuing

loss of SOM is correlated (amongst other factors) to loss of boron (Parker and Parker, 1986) and soon led to the identification of an additional boron deficiency.

The Typic Vitrandepts of the Rotorua region are reported to have adequate nutrient supplies for at least one rotation of *Pinus radiata* (Dyck and Skinner, 1990).

The potential for productivity decline is recognized for all sites (Dyck and Skinner, 1990).

"A high decline susceptability exists for currently very productive sites of inherently low quality and high quality sites with compactable or shallow top soils.

Very low susceptability to productivity decline is indicated for recently deposited coastal sands, since radiata pine growth is almost zero."

Dyck and Skinner (1990) mention in the discussion that

"fertilizer use by crop trees is typically low," and quote (Hart et al. 1986) : "fertilizers can not be regarded as a substitute for organic matter, because, as well as acting as a nutrient reservoir, organic matter improves soil physical and biological properties, which also contribute to site quality and productivity."

The paper concludes with "may":

> "It may be possible to restore productivity...however it may be prohibitively expensive to compensate for the removal of organic matter....The cost of maintaining high productivity by careful management or remedial treatment must be weighed against long-term considerations of the value of site quality."(?!)

This valuation obviously hinges on whether the priority is given to long-term ecological management objectives in agreement with the intentions of the Resource Management Act (R.M.A. 1991), or short-term economical objectives of the boom and bust type.

In 1990, Boomsma and Hunter suggest that experiments should be designed to explore the interactions between genetically improved stock, sites and cultural treatments...and that it may be possible to breed a given species to utilize limited nutritional resources.

Nambiar et al. (1984) is quoted as suggesting that one way was to breed selectively for better root systems so that they may exploit a given soil volume more thoroughly.

Research into the second rotation productivity problem during the 1970's identified a number of practices and influenced managers to adopt those treatments which give dramatic responses.

The management practices that were completely adopted (70-100%) include:

Clearfelling; genetic improvement; chemical weed control; fertilizer application; cultivation (Aust.); windrowing and burning; lower initial stocking; use of basic resource data.

Moderately adopted (10-70%) management practices include:

Inocculation with mycorrhiza; high levels of atrazine; cultivation (N.Z.); Legumes for nutrition.

Minimum adoption (< 10%) of management practices include:

Conservation of organic matter...!

These current management practices consolidate resource exploitation, and management objectives are adapted to the nutrient extraction strategies of pyrophanerophytes.

The inherent capability of mining stored nutrient reserves, which were deposited by the indigenous vegetation was responsible for the economic success of *Pinus radiata*, particularly in the first rotation.

Genetical or "management improvements" might temporarily benefit pyrophanerophyte production in New Zealand, but at the cost that future generations will inherit an inert acid steppe with no potential (Ulrich, 1987).

Thus the management practices and the choice of fire-trees are very detrimental to any long-term perspectives, since they oppose the temperate forest-soil ecosystem strategies based on nutrient cycling and conservation.

The paper (Boomsma, 1990) concludes that the challenge for future research comprises the integration of all processes into a more comprehensive model of the complete water relations of a forest, the necessary inclusion of nutrient components

and that experiments must be designed to explore more fully the interactions between water and nutrients and their effect on tree growth.

The results of this research and that of many cited authors addresses the challenge for future research and elucidates the urgent need for an entirely new approach to forest production management.

Meanwhile, the spread of introduced trees in the New Zealand high country, poses a challenge. The species involved are *Pinus contorta; P. radiata; P. nigra; Pseudotsuga menziesii; Larix decidua; P. sylvestris; P. pinaster; P. ponderosa* and one angiosperm *Acer pseudoplatamus*. All but one of the species involved are conifers and pyrophanerophytes, which account for over 95% of the natural regeneration of introduced species (F.R.I., 1990).

The high combustability of these pyrophyte forests asserts a serious threat to indigenous forests and forest remnants (F.R.I.,1987).

It is therefore necessary to employ early shelterwood harvesting techniques (Janssen, 1991), find a use for the timber (Ledgard and Belton, 1985), and use the shelter of existing trees to diversify the once forested highcountry with re-introduced indigenous (*Podocarpus totara, Nothofagus spp.* etc.) or deciduous trees.

The results indicate that *Acer pseudoplatanus* is a tree that increases the soil fertility and creates a favourable buffer capacity, which increases options for future use.

8.3.5. Re-afforestation research in New Zealand.

The eight tree species recommended for large scale special purpose plantations by the F.R.I (N.Z.F.S., 1981; Glass, 1990) are insufficient and most are inadequate.

The baseline criteria for any plantation will have to be the contribution to soil fertility of a particular tree species. Considering the efficiency of nutrient cycling, only two of the eight are suitable for forest plantations in New Zealand, namely *Acacia melanoxylon* and *Juglans nigra*. The other six are soil nutrient depleting fire-

trees that are unsuitable for sustainable land management objectives and permanent afforestation in New Zealand.

Important research on the ecology, tree establishment and potential for utilization of indigenous forests was summarized in popular books by Salmon, 1980; Wardle P., 1983; 1991, Wardle, J., 1984; Metcalf, 1987; Clifton, 1990; New Zealand Native Forest Restoration Trust, 1992; Brockie, 1992).

The raising of indigenous seedlings is discussed by Pardy and Bergin, 1989 and in F.R.I., 1988.

The transformation of existing exotic forests with shelterwood harvesting techniques and the subsequent establishment of indigenous and deciduous trees in the advantageous shelter of existing unlogged stands is discussed by Janssen (1991-92).

The forest development in canopy gaps in old growth Nothofagus forest is discussed by Stewart et al. (1991), who suggest that the interpretations of response to gap parameters needs to account for differences in disturbance history between sites, which will influence the rate of gap closure.

Gap dynamics and species responses are beginning to be discussed and are illustrated for *Nothofagus fusca* and *N. menziesii* (F.R.I., 1992).

Considerable silvicultural potential has been identified for *Nothofagus fusca* and *Nothofagus truncata* forests (Smale, et al.,1987).

Establishment techniques of podocarps in form of group plantings, are discussed by Beveridge, (1985). It is recommended to use warmer sites for the planting of valuable timber trees, such as *Litsea calicaris, Vitex lucens, Dysoxylum spectabile,* and potentially *Knightia excelsa* and *Elaeocarpus dentatus.*

The bioclimatic definition of 33 representative indigenous forest species and the contemporary forest pattern is discussed and compared with exotic temperate forest systems, in a stimulating paper by Meurk (1995).

Prospects of *Beilschmiedia tawa* for wood production are discussed by Smale, 1986.

In essence, it is unsustainable to harvest existing stands, however, if stands are planted, the time to harvest will be an investment in the future due to tawa's beneficial effect on soil nutrient storage and fertility (Enright and Ogden, 1987).

The potential of growing native trees in plantations is discussed in F.R.I., 1989. It is suggested that the short supply of special-pupose timbers warrants the

establishment of indigenous plantations of *Podocarpus totara; Nothofagus fusca; N. menziesii; Vitex lucens; Litsea calicaris* and *Agathis australis*. A table illustrates how to establish a native species plantation.

It is my suggestion that concern for the soil resource will make the planting of these and other species for future timber production likely and economically justifyable.

Productivity can only be maintained if the natural protective ecosystem strategy of temperate forests is upheld.

8.3.6. Concluding remarks.

Indigenous plants and animals of New Zealand are of the large-bodied, slowly reproducing forms that have proven to be most vulnerable to disruptions (Mark, 1990). Indigenous vegetation co-evolved with birds and invertebrate decomposers of organic material.

Deciduous forests have co-evolved with mammals.

While both vegetation types have in common an apparent symbiosis with a wide range of invertebrate decomposers, a large part of the indigenous vegetation suffers under the pressure of introduced mammals and their high metabolism.

Mammals are now irreversibly established in New Zealand.

It is natural for mammals to depend on the co-evolved primary producers for sustenance.

Planted indigenous-deciduous forests would most likely become the preferred habitat of rodents and ungulates, which will provide additional yield for humans.

However, hunting pressure on mammals in the virgin indigenous forests, would most likely need to continue to achieve a lasting reduction of detrimental mammalian influences on the "unmanaged" indigenous vegetation.

Research in the floristic composition of the plant cover in the Orongorongo study area assured that "foreign plants make no headway into sound standing native forest. Under the closed forest canopy, competition for light and nutrients is intense and the native seedlings appear to be so well adapted to the situation that foreign plants can not establish a foothold"(Brockie, 1992). This observation is encouraging with regard to the future integrity of the virgin indigenous forests and also gives

some indications towards a possible temporal sequences of species in mixed, managed forests.

9 Conclusion.

This research provides prove of divergent treegroup strategies, and gave indications on individual nutrient cycling strategies.

In accordance with the results and in agreement with the estimations of this research;

Ulrich (1987) suggests that:

> "Trees like *Picea abies* and *Pinus radiata* eliminate themselves by rapidly changing the soil state, which is the reason why evolution did not lead to the dominance of fast-growing tree species."

The problem of pyrophyte tree plantations relates to their inherent unsustainability.

Pyrophanerophytes in plantations feed on the accumulated elasticity of the indigenous forest-soil ecosystem, which, common to most temperate regions, evolved during the holocene.

The data has also elucidated the species- and association specific capacity to maintain a forest-soil ecosystem at the state of highest possible elasticity and will be of extreme importance for the planning of future protective production forest-ecosystems.

The research results are very encouraging and warrant future research to gather data on species- and association specific plant litter qualities and the species- or genera specific effectiveness in altering the soil nutrient storage capacity.

There is a need to gather far more knowledge on the nutrient cycling responses of individual genera or species to various mineral substrate compositions and to climatic factors.

This information needs to be gathered rapidly, since it could accelerate the generative processes and significantly improve the potential for yield of planted forests, established for production and the sustainable management of lands.

Comprehensive research on the nutrient cycling responses of species on various substrates should accompany planting programs.

Forest planting programs should meanwhile be based on available information on the natural potential distribution of tree species and their adaptations to environmental parameters.

9.1 The relative importance of Soil parameters for the estimation of nutrient cycling dynamics .

9.1.1 Soil pH

The simplest field methods that give rapid indications on the condition of the soil, and the processes within the soil, as a result of plant litter input, include the measurement of soil pH and soil organic matter at various soil depths within the A-horizon and of soil pH within the B-horizon. The difference between both, A and B horizons should give a clear indication on the nutrient cycling strategy of the phanerophyte.

9.1.2 Carbon and Nitrogen

Both carbon and nitrogen require biological fixation and are important indicators of the effects of the biota on the soil.

Soil carbon can frequently be estimated from the amounts of soil organic matter. Its incorporation into the soil medium may be an important indicator for bioturbation and biotic activity, which is associated with favourable autotrophic inputs. Carbon may however also derive from organic litter leachates (phenolic and fulvic compounds) and root-exudates that are primarily proton carriers and that serve with the mobilization and extraction of mineral nutrients. A soil organic matter -, or carbon analysis on its own has therefore little qualitative potential to predict certain nutrient cycling responses.

Soil nitrogen is entirely dependent on the composition of the biota for fixation and incorporation into the soil medium. It usually is a product of a symbiosis between autotrophs and heterotrophs in a non acidic soil-environment. The N-fixation process requires a considerable amount of biotic energy and is an important element of a coherent ecosystem. Amounts of Nitrogen are therefore generally very limited under the influence of acidifying tree species that are adapted to the extraction of soil nutrients.

The following soil parameters seem to be most useful for a comparison of the cycling effects of autotrophs and associated heterotrophs on the mineral soil.

9.1.3 Cation exchange capacity, Exchangeable bases and Base saturation.

The cation exchange capacity (C.E.C.), the total exchangeable bases (T.E.B.) and the base saturation (B.S.) constitute three essential soil parameters, which however require soil laboratories for analysis.

The mineral contribution to each soil parameter should be known for a comparative research on the effects of different primary producers.

The additional C.E.C. then represents the organic contribution, derived from the biological fixation of gaseous matter, and the additional T.E.B. represent the minerals that have been cycled and stored. The base saturation is then an indicator of the balance of the organo-mineral life complex.

In the case of this study, previous research provided the base line data (Tomlinson and Leslie, 1977).

In order to correctly interprete a variety of nutrient cycling tendencies, it is important to evaluate organic increases in C.E.C., together with the base saturation and the T.E.B.

The following points need to be considered, when soil parameters are compared and plant influences estimated:

1) The organic input to soil may be low, due to sparse vegetation (Calluna vulgaris); impeded decomposition or rapid mineralisation of organic matter (through fire). Under such conditions the C.E.C. and the T.E.B. will largely be mineral based and low, but could have a high base saturation, especially in an arid environment.

2) A high organic litter production may be associated with a low decomposability, which results in a limited organic exchange capacity (primarily as mobile proton carriers) and is usually associated with low levels of T.E.B. and a low base saturation.

3) The phytomass litter-production may be high and fairly decomposable, resulting in a significant increase of the C.E.C. on humic material. If the nutrients are either, retained by the phytomass and/or immobilized by the microbial biomass, both the level of T.E.B. and the base saturation remain low. A majority of exchange sites is occupied by hydrogen ions.

4) Substantial increases, of both C.E.C. and T.E.B. over and above the mineral contribution can predominantly be associated with organic input from the phytomass, which is readily decomposeable. Net nutrient mineralization is associated with temporary nutrient immobilization by the soil biota, and a general increase of the soil buffer capacity, due to the formation of soil aggregates and soil humus.

These points describe the three soil parameters under various environmental conditions. They can be used to assess major nutrient cycling strategies of the main primary producers and are apparent under the trees of this study. The Pinatae and eucalypts can be associated with points 1 and 2. The indigenous and exotic deciduous trees feature individuals that affect the soil as described in point 3 and 4 with regard to the three soil parameters. Stratified soil sampling and analyses on key parameters should rapidly increase our knowledge of individual nutrient cycling tendencies on various substrates and with varying mineral availabilities.

9.1.4 The Humic fractions.

C.E.C. increases are generally linked to increases in humic matter.

There are qualitative and quantitative differences in the humic matter fractions, produced by different associations (Kononova, 1966; Koegel-Knabner, 1992). The diversity of the humic fractions, their qualitative differences and their longevity, reduce the usefulness of quantitative estimations for individual plant strategy comparisons. Their longevity however corresponds to ecosystem and plant association dynamics (canopy and subcanopy; gap-dynamics etc.) and analyses of humic fraction qualities and quantities are useful for the comparison of the dynamics of associations within ecosystems.

9.2   The Individual and the Association

In the same way that individual autotrophs form symbioses with heterotrophs to fix nitrogen, other individuals are likely to accumulate and cycle other elements (e.g. phosphorus).

All individuals together ensure that elements are efficiently utilized and cycled for the benefit of the progeny and the stability of the ecosystem.

Humans are just about to grasp this concept (R.M.A., 1991).

It is well established that each plant has evolved specific tolerance levels with regard to the range of inherent requirements for nutrients, water and light (Grime,1979, Wilmanns, 1984).

Dependent on the mineral availability of the substrate, the litter mineral contents vary between individual plants of the same species (Roehrig, Ulrich, 1991).

However, within the limitations of the site, each plant complexes organic and mineral matter in its specific way and thereby strongly influences the composition of the soilbiota and the direction of soil genesis.

It must be emphasized that plant nutrient cycling strategies are inherent (Ulrich,1987; Koegel-Knabner, 1992) and that variations in mineral substrate composition and fertility, shorten or extend the time for soil recovery.

Individual plants typically occupy spatial and temporal niches, irrespective of whether the ecosystem is in a phase of succession or dynamic equilibrium.

In the first instance an individual plant provides the soil organic matter, the nutrient storage and the shelter, required by its successor. If the ecosystem is in the steady state or dynamic equilibrium phase, it has reached a phase of protective stability, by providing protection for each individual against environmental extremes (Odum, 1983; Larcher, 1984).

A gap dynamic ensures the temporal replacement of species and changes in litter quality encourage a dynamic soil evolution towards increases of ecosystem elasticity.

The system is co-dependent and cooperation is the primary force (Odum, 1983), as evidenced by efficient nutrient cycles.

The following explains the main differences between individual organisms and the encompassing ecosystem.

The characteristic features of organisms relate to their ability for genetical and behavioural change, which is encouraged by both,

the cooperation;

> of its parts (cells; organs)

> or individuals of the same species (social behaviour; suckering, group formation)

or of different species (symbioses, commensalism)

and the competiton between organisms.

The unique property of ecosystems is to combine autotroph and heterotroph organisms in such a way that the effects on the environment are balanced out within the system. This property is a consequence of the self-organization of open systems in steady state, according to the principles of irreversible thermodynamics (Ulrich, 1987).

9.3   Management Strategies

"In forestry, but also in agriculture, or generally speaking in landscape management, man is always dealing with ecosystems. This fact has been neglected by both research and practical management, which usually focusses on populations (for example; a crop and its pest).

In consequence, the characteristic properties of ecosystems, like matter balance and the maintenance of the chemical state are neglected.

The problem with this kind of approach begins if the long-term effects of ecosystem development under natural stress or under management come into focus. Long-term means periods of decades and centuries"(Ulrich 1987).

Such periods are of great concern to humanity and are beginning to be addressed by the intentions of the Resource Management Act, (1991).

The results (chapter 6) provide proof of the importance of the choice and the temporal and spatial distribution of tree species, and give encouragement for a new focus for land management decisions that has yet to be based on the principle of sustainablility.

There is a need to acknowledge:

1) That soil degeneration is more than just visible soil erosion, but involves in both, unforested land and in land covered by fire trees (in particular the genera *Pinus* and *Eucalyptus*), the rapid and continual loss of nutient storage

capacity, associated with the loss of soil organic matter of the mull humus type and a corresponding shift away from the preferred silicate buffer range.

2) That the loss of soil organic matter can not easily or fast be remedied (artificial fertilization is of little use without S.O.M. of the mull humus type).

3) That site rehabilitation is a continuous and basic life process, which is based on the spatial and temporal species diversity in forest ecosystems.

The principle of ecosystem organization is the minimization of entropy and applies to any site rehabilitation.

4) That this realisation urgently calls for new decisive directions in forest- and land management, that need to be bioregionally initiated.

5) And that an understanding of nutrient cycling processes is essential for any future forest manager,

so that the current de-coupling of nutrient cycles,

the continued reduction of nutrient storage and

the subsequent destabilization of forest-soil ecosystems can be avoided in future.

This research provides a basis from which new and necessary land management directions may evolve.

These may lead to an eventual sustainability of production, within the elasticity range of the ecosphere and its component ecosystems and may thus encourage the re-integration of a future human culture with the ecological processes of this planet.

10 An Ecological Recommendation.

Odum (1983) cites an appropriate analogy between the evolution of ecosystems and society.

> "At the young pioneer stage, both, natural and cultural systems are characterized by high birthrates, rapid growth, high economic returns and the utilisation of any available resources. As the pioneer stage reaches the limits of growth the evolution directs both systems from resource exploitation based on individualism (fire trees; feudalism; materialism) towards symbioses (citizen rights; equality; the welfare state) and the recycling of resources."

This analogy can even be extended to the stages of the ontogeny of organisms. If we compare the evolution of human society with the ontogenetic development of its component individuals, we find that there are interesting parallels between the physical and psychological development of an individuum from puberty to maturity and a human society, which is just initiating the process of maturation by recognizing its responsibilities, not only to its own descendants (Brundtland report; RMA 1991) but, hopefully very soon, also to the functioning of the ecosystems on this planet (MfE, 1993).

The **future of humanity** will rely on its ability to develop a mature relationship with the environment, based on a **symbiosis between the cultures of humanity and the ecosystems** of the ecosphere.

Humans have in the past achieved many forms of symbioses with individual species, but rarely achieved a balance with, particularly forest ecosystems.

The domestication of numerous plants and animals and at the same time the devastation of forest, wildlife and soils in the mediterranean and the podzolization of soils in Western- and Central Europe, are historical examples.

The matter balance of ecosystems has most frequently suffered severe exploitation under human influence. With the world wide expansion of materialism, many symbioses have degenerated to parasitic relationships. The parasitism on other lifeforms is based on the channelling of vast amounts of matter and energy into the human sphere. Most of this production does not necessarily satisfy human needs but the consumerism of a world wide and detached urban society.

Other life forms which had not yet been exploited have suffered- or are on the brink of extinction and mounting efforts are put into the creation of refuge space for endangered species.

This refuge space, intentionally created for the benefit of endangered life forms and usually gazetted as National Park, remains under marketing pressure. Civilization refugees feel the need to experience the essence of life (ecotourism). Mounting numbers of thrillseeking tourists feel the need to escape and direct the marketing of experience to ever more wasteful fashions (helicopter sight-seeing, - skiing, speed-boating etc.).

The urgency for the preservation of representative ecosystems in New Zealand was addressed by Mark (1980), who clarifies that

"The diversity of New Zealand's environment provides a wide range of alternatives for man's use, but a clear understanding of each feature and its inter-relationship with others is a prerequisite for wise land use decision making."

He stresses the shortcomings in multiple-objective planning and development with the persistence of two serious problems:

A) insufficient trained environmental planners and managers to ensure that adequate evaluation of the complexities of ecological systems...takes place

and B) the narrow range of objectives of many government agencies.

Dingwall is quoted as emphasising the need for ecological principles to take priority over present land tenure and use ... and thereby overcoming the real danger that protection status will be increasingly accorded only to our economically useless and otherwise unwanted landscapes.

These issues were finally addressed with the surveys of the Protected Natural Areas Program (P.N.A.P., 1987).

The P.N.A.P has since been instrumental in the identification the intrinsic ecological diversity of New Zealands ecological districts and serves as a first important base line study for the recognition of threats to the indigenous biota of the districts.

Extermination threats to the indigenous lowland forests were halted by the N.Z. Forest Accord, 1987.

The division of land into protection and production (exploitation), as agreed upon by the N.Z. Forest Accord, 1987, has been an important temporary measure to delay a pending environmental catastrophy.

However, according to the principles of ecosphere and ecosystem organization, human society has to rapidly adopt the ecosystem strategies of minimizing entropy production in the management of resources.

A human-ecosystem symbiosis is required, where resource decisions are based on the matter balance of the ecosystems and are formulated and assessed bioregionally, or within the identified ecological districts and regions.

The results give evidence that the nutrient cycling strategies of both indigenous and deciduous vegetation are of high benefit for the improvement of soil quality and hence for an economical and truely sustainable forestry.

Production will need to be nested in a protective forest ecosystem, with the highest possible elasticity, stability and resilience.

Sustainable forest plantation management therefore includes the shelterwood transformation of fire tree plantation forests, the afforestation of bare land and the inclusion of trees into the cropping landscape of annuals and perennials.

The establishment of tree species on a variety of substrates and under a variety of climatical conditions requires experience and knowledge.

While some knowledge is available, there is a definite lack of experience with regard to the requirements of a number of species.

It is well known that most forest species require shelter from existing trees, rather than competition from shrubs for successful establishment.

Therefore, the transformation away from fire tree plantations needs to proceed according to shelterwood harvesting techniques, which have been devised as more appropriate methods of tree harvest in the temperate forest biome (F.R.I., 1983; Janssen, 1991, 1992; Dengler, 1992).

The common denominator for the choice of tree species in any landscape should always be its potential to improve the site.

Considerations on the productivity and multiple use of indigenous and exotic deciduous tree species have to be identified locally (coppice, timber, fruits, nuts, tourism, medicines, meat etc.) and intrinsic values need to always be considered on par.

The eight tree species, *Acacia melanoxylon Juglans nigra* and six species of the genera *Eucalyptus* and *Pinus*, that have been recommended for large scale special purpose

plantations by the F.R.I (N.Z.F.S., 1981; Glass, 1990) are insufficient and the pyrophanerophytes are inappropriate.

The baseline criteria for any plantation will have to be, whether a particular tree species contributes to soil fertility. Considering the efficiency of nutrient cycling, only two of the eight species are suitable for forest plantations in New Zealand, namely *Acacia melanoxylon* and *Juglans nigra*. The other six are soil nutrient depleting fire-trees that are unsuitable for sustainable land management objectives and for permanent production based afforestation in New Zealand.

Based on the observations, described in chapter 3, and the results, discussed in chapter 6, it is suggested that

a combination of deciduous canopy genera

> *Acer, Aesculus, Fraxinus; Plagianthus; Tilia; Ulmus*

and indigenous (sub)-canopy species

> *Fuchsia excorticata; Sophora microphylla; Melicytus ramiflorus; Pseudopanax arboreus; Ripogonum scandens; Elaeocarpus dentatus; Beilschmiedia tawa* (Enright & Ogden, 1987)

is particularly useful for the rapid natural re-vitalization of semi-degraded land.

Additional species that can be considered to be rapid soil enhancers include: the pioneer species

> *Aristotelia serrata, Coriaria arborea,* (Brockie, 1992) *Coprosma* spp., *Olearia* spp.,

and also most likely the indigenous spp.:

> *Cordyline* spp., *Entelea arborescens, Hoheria populnea, Nestegis cunninghamii, Pennantia corymbosa, Rhopalostylis sapida, Schefflera digitata,* (amongst others).

and additionally the exotic deciduous genera

> *Alnus, Betulus, Castanea, Cornus, Crataegus, Juglans, Morus, Populus, Prunus, Pyrus, Ribes, Sambucus, Sorbus* (Hofmeister, 1983, Mikola, 1985), and *Diospyros, Liriodendron.*

The species and the genera

> *Coriaria arborea, Grisellinia littoralis, Kunzea ericoides, Leptospermum scoparium, Myoporum laetum; Carya* spp., *Quercus* spp., *Morus* spp. and *Podocarpus totara* a.o.

will be useful for the establishment of forest on exposed land.

A permanence to the improvement of the soil elasticity will be achieved by the humic matter contributions of intermixed indigenous emergent species such as species of the

> Podocarpaceae and canopy trees like *Metrosideros spp., Nothofagus spp. Weinmannia racemosa; Knightia excelsa, Phyllocladus, Vitex,* (Enright & Ogden, 1987) *Acacia, Carpinus; Fagus grandifolia, Quercus spp. Nyssa,* (Qualls, et al., 1991), *Robinia, Metasequoia, Sequoia.*

The results, discussed in chapter 6 support the assumption that a forest-soil ecosystem flourishes naturally with the incorporation of a diverse range of specialist nutrient cycling plants.

The correlations indicate that each species fills a niche in the cycling of nutrients. Interspersed species with litter that resists decomposition produce plenty of humus material, which, in co-operation with the rapidly decomposing, mineral rich litter of (e.g. *Melicytus ramiflorus*) creates the best possible storage capacity for a particular site. Thus, the combined litter of each species contributes to the elasticity of a lowland forest ecosystem.

> The managerial task of the new forester consists of establishing the optimal spatial and temporal sequence of species in a given environment, to rapidly increase the potential for yield, by facilitating seedling establishment and guiding the natural rehabilitation.

A predominance of Nothofagus species (*N. menziesii; N. solandrii var. clffortioides*) in montane forests sheds litter that resists decomposition, due to both, the climate and the litter composition. The decomposition products are of the kind described by Kononova (1966), as typical of the boreal taiga zone (highly mobile fulvic acid like humic acids).

On its own, the predominance of organic material from a single species in these climatic conditions, does not induce a favourable buffer range that could create a topsoil with a high elasticity. This is not necessary in such an environment, in which climatic conditions and ectomycorrhizal activities advance a high rate of mineral weathering.

The single canopy species montane beech forests are ecologically entirely different and not comparable to any type of indigenous lowland forest ecosystems.

Hence, an argument in favour of the "naturalness"of soil depleting fire tree species as a lowland monoculture rests on misinformation and is misleading.

In recapitulation, land and forest management decisions should be based on the following priorities:

> to advance soil-generation, -elasticity and -rehabilitation and to arrest soil degeneration, -erosion;
>
> by utilizing the existing shelter to transform the forested plantation landscape of pyrophanerophyte monoculture
>
> from a short term productive stage, based on soil resource exploitation
>
> to a protective stage, in which production is intensively and locally managed
>
> and the potential for yield permanently secured.

This can be achieved by uniting indigenous and deciduous forest vegetation and utilizing various species and trees at different ages for miscellaneous purposes on production land.

This transformation can not be left to rely on current world marketforces, because of temporal differences of life expectancies of the market system, which is adjusted to the lifetimes of individual humans, and that of forest ecosystems, which on a temporal scale can only compare to the evolution of human communities, consisting of several generations.

The concept of the Commons, familiar to the ancestors of both, Europeans and Polynesians, may need to be re-defined in the context of the ecosystem, and established within the bioregions or ecological districts of New Zealand. This may provide a solution to many of todays social and ethnical problems.

The establishment of a productive, communal forest ecosystem will join communities together in an effort to increase the resource base for future generations, while at the same time expecting moderate returns as the system grows.

Local Council and Community incentives might include communal or fiscal wage payments to landowners for the planting and tending of mixed species afforestation, coupled to increases in land valuations and decreases in taxation on land. The communal investment could be regained at the time of harvest, by claiming a percentage of the timber value. Flow on effects will include sensible employment

opportunities, based on the addition of value to the raw material and the local manufacture of goods.

Once the forest ecosystem is established, the benefits to the community will be enormous. High elasticity of the forest soil ecosystem, increased employment, wisdom, perpetual income, aesthetic values, etc.

Unsustainable land management practices could be phased out by national or local stipulations that encourage a mixed species transformation of the large scale rotation plantations of pyrophanerophytes. There is a need to raise public awareness. Increasing the taxation to discourage land exploitation, coupled to a simultaneous decrease of land value might help to turn the scale towards sustainable land management.

As a guideline, the diversity of the prehistoric indigenous lowland forest could serve as an example for the desired species diversity of a managed production forest ecosystem.

A software package called PLANTGRO (Hackett, 1991) has recently been introduced to increase the limited amounts of human knowledge on the environmental requirements of most plants (Grime, 1988) and to facilitate the sharing of knowledge gained and retrieved and to increase human experience with regard to plant environment responses.

A series of gap-models has been developed to forecast the temporal succession of mixed forests.

The FORET model (Shugart and West, 1977) simulates 33 species in a southern Appalachian forest.

The JABOWA model (Botkin et al. 1972) simulates forest dynamics that are associated with 13 species found in the north-eastern American hardwood forest.

The KIAMBRAM model (Shugart et al. 1980) simulates the dynamics of 125 species that are found in the sub-tropical rainforest in the vicinity of the New South Wales - Queensland border in Australia, amongst other models.

The latest developments are concerned with the simulation of ecosystem responses. The models are individual-based vegetation simulators and compartment models of nutrient cycling and soil water relations. Applications focus on interactions and

feedbacks between vegetation structure (species composition, size structure) and ecosystem processes (water balance, nutrient cycling), and how these relationships vary across environmental gradients. The model allows for the computation of fully coupled ecosystem models, which consist of a vegetation model, the soil water model and the nutrient cycling model (Lauenroth et al., 1993).

Human experience with forest dynamics is often limited, due to the different life spans of trees and humans.

Temporal and spatial movements of tree species during the holocene have been highlighted by pollen analyses of lake deposits (Delcourt, 1987) and are helpful in providing an image of the natural dynamics of species strategies and migrations, which, together with publications on plant- and ecosystem dynamics (Hofmeister, 1983; Ovington, 1983; Wardle, 1984; Walter, 1985, 1987; Waring, 1985; Mollison, 1988; Grime, 1988; Roehrig, 1991; Dengler, 1992) will be helpful with the re-establishment of temperate forest ecosystems.

The concluding recommendation is that;

further research on the plant-soil interactions,

the timely publications of comprehensive information on plant and ecosystem dynamics,

and the development of the PLANTGRO-; the GAP models; and the COUPLED ECOSYSTEM computer software programs

will facilitate the successful planning and planting of complex and resilient, protective and productive forest ecosystems.

Moreover,

No computer program will ever replace

the human need for the attainment of

life experience and wisdom

contained within

a vibrant forest ecosystem.

References:

Abee, A. and Lavender, D. 1972. Nutrient cycling in throughfall and litterfall in 450-year-old douglas-fir stands. In: Proceedings-Research on Coniferous Ecosystems-A Symposium.

Adams, J.A., 1976. Nutrients requirements of four Nothofagus species in north Westland, New Zealand, as shown by foliar analysis. N.Z. J. Bot., 14: 211 - 223.

Adams, J. A., 1978. Long-term aspects of nutrient loss from forest soils and ecosystems. N.Z. Journal of Forestry, pp.12-20.

Allaby, M., 1994. The Concise Oxford Dictionary of Ecology. Publ. Oxford University Press. 415 p.

Allen, R.B., Johnson, P.N., 1982. Vegetation of the Townbelt. Department of Scientific and Industrial Research, Botany Division.

Allen, S.E., Grimshaw, H.M., Rowland, A.P., 1986. Chemical analysis. chapt. 6. In: Methods in Plant Ecology. eds. Moore & Chapman, second ed. Blackwell. pp. 285-344.

Andreux, F. G. et al., 1990. Humus contents and transformations in native and cultivated soils. Centre de Pedologie Biologique, Vandoeuvre-les-Nancy Cedex, France; Centro de Energia Nuclear na Agricultura, Universidade de Sao Paulo, Brasil. In: The Science of the Total Environment, 90: 249 - 265.

Bagnal, R.G., 1972. The dry weight and calorific value of litter fall in a New Zealand Nothofagus forest. N.Z. J. Bot., 10: 27 - 36.

Baker, T. G., Oliver, G. R., Hodgkiss, P. D.,1986. Distribution and Cycling of Nutrients in Pinus radiata as affected by past Lupin Growth and Fertiliser. In: Forest Ecology and Management, 17, 169-187.

Baum U., 1975. Stickstoff-Mineralisation und Stickstoff-Fractionen von Humusformen unterschiedlicher Waldoekosysteme. Goettinger Bodenkd Ber. 38:1-96.

Baumeister, W., et al. 1975. Das grosse illustrierte Pflanzenbuch. pp. 1654. Bertelsmann Lexikon Verlag, Guetersloh, Berlin.

Baylis, G.T.S., 1975. The magnolioid mycorrhiza and mycotrophy in root systems derived from it. In: Saunders, Mosse & Tinker (eds.), Endomycorrhizas. Academic Press, London, pp. 383 - 389.

Benson, W.N. 1959. Dunedin Volcanic Complex. In Fleming, C.A. (Ed.): Lex. stratigr. int. 6 (Oceanie) (4):91-3.

Benson, W.N. 1968. Dunedin district 1 : 50,000. N.Z. geol. Surv. Misc. Ser. Map 1. DSIR, Wellington.

Beveridge, A. E., 1964. Dispersal and distribution of seed in central North Island podocarp forest. Proc. N.Z. Ecol. Soc., 11: 48 - 55.

Beveridge, A. E., 1973. Regenration of podocarps in a central North Island forest. N.Z. J. For., 18: 23 - 35.

Beveridge, A. E., Bergin, D. O., Pardy, G. F., 1985. Planting podocarps in disturbed indigenous forests of the central North Island. In: N.Z. Journal of Forestry, 30 (1): pp.144-158.

Bieleski, R.L., 1959. Factors affecting growth and distribution of Kauri (Agathis australis salisb.). Aust. J. Bot., 7: 252 - 294.

Black, C. A., 1975. Methods of Soil Analysis. (Ed.) Black, C. A., Chapter 5.4.1 Organic carbon, pp. 315-316; Description of method by Kalembasa & Jenkinson, 1973. Publ., American Soc of Agronomy Inc.

Blair, J. M., 1988. Nitrogen, Sulfur and Phosphorus Dynamics in Decomposing Deciduous Leaf Litter in te Southern Appalachians. Soil Biol. Biochem. Vol. 20, No.5. pp. 693-701.

Boland, D.J., et al. 1985. Forest Trees of Australia. Nelson . C.S.I.R.O. Government Print. pp 686.

Bond, R. D., 1960. The occurrence of microbial filaments in soils and their effect on some soil properties. C.S.I.R.O. (Aust.) Divn. Soils Divn. Report 10/60, p.9.

Boomsma, D. B., Hunter, I. R., 1990. Effects of Water, Nutrients and their Interactions on Tree Growth, and Plantation Forest Management Practices in Australasia: A Review. In: Forest Ecology and Management, 30, pp. 455-476.

Botkin, D. B., Janak J. F., Wallis, J.R., 1972a. Some ecological consequences of a computer model for forest growth. J. Ecol. 60: 849-873.

Botkin, D. B., Janak J. F., Wallis, J.R., 1972b. Rationale, limitations and assumptions of a northeastern forest growth simulator. IBM J. Res. Develp. 16: 101-116.

Brockie, R.,1992. A Living New Zealand Forest; A Community of Plants and Animals. Publ. David Bateman. 172 p.

Brockman, F., Merrilees, R., 1979. Trees of North America. pp. 280. Golden Press New York.

Bruntland, G.H. et al., 1987. Our Common Future. World Commission on Environment and Development. Oxford Univ. Press.

Calderoni, G., Schnitzer, M., 1984. Effects of age on the chemical structure of paleosol humic acids and fulvic acids. Chemistry and Biology Research Institute Department of Agriculture, Ottawa, Canada. In: Geochimica et Cosmochimica Acta, Vol. 48: 2045 - 2051.

Campbell, I.B., 1970. A weathering sequence of basaltic soils near Dunedin. New Zealand. Soil Bureau, Department of Scientific and Industrial Reseach, Lower Hutt, New Zealand. New Zealand Journal of Science 14: 907-924.

Chen, Y., Senesi, N., Schnitzer, M., 1978. Chemical Degradation of Humic and Fulvic Acids, Extracted from Mediterranean Soils. Soil Research Institute, Department of Agriculture, Ottawa, Canada. In: Journal of Soil Science, Vol. 29: 350 - 359.

Chu-Chou, M., Grace, L. J., 1990. Mycorrhizal fungi of radiata pine seedlings in nurseries and trees in forests. In: Soil biol. Biochem. Vol. 22, No. 7, pp. 959-966.

Clifton, N. C., 1990. New Zealand Timbers. Exotic and Indigenous. The Complete Guide. pp.170. N.Z. GP Books.

Climate, .tst; 2, 1994. UIC Geogrmj VAX/VMS Version V5.5-2 Computing Services Centre, University of Otago.

Coombes, A.J., 1992. World Trees. The visual guide to over 500 species of tree from around the world. Collins Eyewitness Handbooks. pp 320.

Coombs, D.S. 1987. Dunedin Volcano. GSNZ Field Trip A1 Geology Department, University of Otago.

Coombs, D.S. and Wilkinson, J.F.G. 1969. Lineages and fractionation trends in unsaturated volcanic rocks from the East Otago volcanic province (New Zealand) and related rocks. J. Petrology 10: 440-501.

Cooper, K.M., 1976. A field survey of mycorrhizas in New Zealand ferns. N.Z. J. Bot.., 14: 169 - 181.

Cowan, P.E., Waddington, D.C., Daniel, M.J., Bell, B.D., 1985. Aspects of litter production in a New Zealand lowland podocarp / beech forest. N.Z. J. Bot. 23: 191 - 199.

Daniel, M.J., 1975. Preliminary account of litter production in a New Zealand lowland podocarp-rata-broadleaf forest. N.Z. J. Bot. 13: 173-87.

Daniel, M.J., Adams, J.A., 1984. Nutrient return by litterfall in evergreen podocarp-hardwood forest in New Zealand. N.Z. J. Bot.: 22.

Department of Survey and Land Information. Topomap Series I44, 1987, NZMS 260 I44&J44 Dunedin, Edition 2.

Daubenmire, R., 1978. Plant geography with special reference to North America. New York.

Delcourt, P.A. and Delcourt H.R. 1987. Long-Term Forest Dynamics of the Temperate Zone. Ecological studies: Springer-Verlag V.63; 450p.

Dengler, A., 1992. Waldbau auf oekologischer Grundlage. 1. Band: Der Wald als Vegetations form und seine Bedeutung fuer den Menschen. pp 350.

2. Band: Baumartenwahl, Bestandesbegruendung und Bestandespflege. pp. 314. Verlag Paul Parey, Hamburg und Berlin.

Dickinson, K.J.M., Mark, A.F., 1988. The New Zealand Protected Natural Areas Programme - A Progress Report. Proceedings of the ANZAAS Centenary Congress Sydney. Univ. of N.S.W. Australia

Dugdale, J. S., 1974. Arthropod species composition of the beech forest floor. Beech Research News 1: 25-27.

Dugdale, J.S., 1977. Phytophagous insects and their hosts. In: Symposium on Pest-Plant Relationships. N.Z. Entomol., 6: 213 - 243.

Dunedin City Council, Forestry Department Flagstaff, 1987. Sheet Reference Number: NZAM 808/2; Photography S/N 7714.

Dyck, W. J., Will, G. M., Messina, M. G., 1985. The influence of radiata pine on soil. Proceedings of the soil Dynamics and land use seminar, Blenheim. pp.263-287.

Dyck, W. J., Skinner, M. F., 1990. Potential for productivity decline in New Zealand Radiata Pine Forests. pp.318-332. In: S.P. Gessel, D.S. Lacate, G.F. Weetman and R.F. Powers. Sustained Productivity of Forest Soils. Proceedings of the 7th North American Forest Soils Conference. University of British Columbia, Faculty of Forestry Publication, Vancouver, B.C. 525p.

Ellis, R.C., 1971. The mobilization of iron by extracts of *Eucalyptus* leaf litter.

J. Soil Sci. 22. 8-22.

Ertel, J.R., and Hedges, J.I., 1984. The lignin component of humic substances: Distribution among soil and sedimentary humic, fulvic, and base insoluble fractions. Geochim. Cosmochim. Acta 48: 2065-2074.

Eyre, F.H., 1980. Forest cover types of the United states and Canada. Soc. Am. For. Washington D.C.

Fahey, T. J., Knight, D. H., 1986. Lodgepole pine ecosystems. Bio Science 36:610-616.

Falkengren-Grerup, U., Tyler, G., 1993. Experimental evidence for the relative sensitivity of deciduous forest plants to high acidity soils. In: Forest Ecology and Management, 60, pp. 311-326.

Falla, R.A., Sibson, R.B., Turbott, E.G., 1987. Collins guide to the birds of New Zealand and outlying islands. Collins Auckland; London. p. 247.

Felbeck, G. T., 1971. Chemical and Biological Characterization of Humic Matter. In: Soil Biochemistry; Mc Laren (eds.) Vol. 2; 3: 36 - 59.

Flaig W., Beutelspacher H., Rietz, E., 1975. Chemical Composition and Physical Properties of Humic Substances. In: Soil Components Vol.1 Organic Components; Gieseking, J. E. (ed.), Springer Verlag.

Fleming, C. A., 1977. The History of Life in New Zealand Forests. N.Z. Journal of Forestry. 1977: pp. 249-262.

Floges, 1980?; from appendix A-2. Die Florengeschichte und Paläoökologische Stellung der Coniferen des West Malayischen Archipels. Publ. ? pp.119 - 135.

Forests Commission Victoria, 1984. Map of Forests of Victoria. Department of Conservation, Forests and Lands, Div. of Forest Management, Victoria Australia.

Forest Research Institute, 1983. Interplanting. What's new in forest research. F.R.I. No. 121.

Forest Research Institute, 1987. Reforestation after fire in Canterbury beech forests. F.R.I. No.149.

Forest Research Institute, 1987. Management prospects for tawa. F.R.I. No. 153.

Forest Research Institute, 1988. Raising native trees and shrubs from seed. F.R.I. No. 158.

Forest Research Institute, 1989. Growth of native trees in plantations. F.R.I. No. 173.

Forest Research Institute, 1990. The spread of introduced trees in the New Zealand high country. F.R.I., N.Z., No. 203.

Forest Research Institute, 1992. Structure and regeneration of mixed beech forests. F.R.I. No. 213.

Franke, W., 1981. Nutzpflanzenkunde. Nutzbare Gewaechse der gemaessigten Breiten, Subtropen und Tropen. pp 470. Thieme Verlag.

Franklin, D.A., 1968. Biological Flora of New Zealand. 3. Dacrydium cupressinum. Lamb. (Podocarpaceae) Rimu. N.Z. J. Bot., 6: 493 - 513.

Fredriksen, R.L. 1972. Nutrient budget of a Douglas-fir forest on an experimental watershed in western Oregon. In: Proceedings-Research on Coniferous Forest Ecosystems-A symposium.

Froude, V.A., 1980. The allelopathic potential of some abundant New Zealand forest and scrub plants. Ecology Division Report. (unpublished). 18 p.

Gatto, M., Rinaldi, S., 1986. Some models of catastrophic behaviour in exploited forests. ?In: Ecol. Model. Accepted 19.8. 1986: pp. 213-222.

Gayler, W., 1985. Umbau von Reinbestaenden in naturgemaesse Wirtschaftswaelder. A.F.Z. 18: pp.443-445.

Ghosh, K., Schnitzer, M., 1980. Macromolecular Structures of Humic Substances. Chemistry and Biology Research Institute Department of Agriculture, Ottawa, Canada. In: Soil Science, Vol. 129 No. 5, pp. 266 - 276.

Glass, B. P., 1990. Wood production for specific uses - a market-oriented approach. N.Z. Forestry, 1990.

Goh, K. M., Heng, S., 1987. The quantity and nature of the forest floor and topsoil under some indigenous and nearby areas converted to *Pinus radiata* plantations in South Island New Zealand.

Gorer, R., 1976. Trees and Shrubs. A complete guide. Newton Abbot London; North Pomfret (VT) Vancouver, pp. 264.

Grime, J. P., 1979. Plant Strategies and Vegetation Processes. Unit of Comparative Plant Ecology, Department of Botany, University of Sheffield. Publ. John Wiley & son. 222 p.

Grime, J.P., Hodgson, J.G., Hunt, R., 1988. Comparative Plant Ecology. A functional approach to common British species. Unwin Hyman London, pp 699.

Groombridge, B., 1992. Global Biodiversity. Status of the Earth's Living Resources. Report by the World Conservation Monitoring Centre, Chapman & Hall, p. 585.

Grubb, P.J.; Green, H.E. and Merrifield, R.C.J. 1971. The ecology of chalk heath: its relevance to the calcicole-calcifuge and soil acidification problems. J. Ecol. 57: 175-212.

Hackett C., 1991. Plantgro. A Software Package for Coarse Prediction of Plant Growth. CSIRO Publications Australia.

Hamaker, Weaver, 1983. Stopping the coming Ice age. Global climatic cycles; Rock mineralisation; Plant-mineral interactions. Video, U.S.A.

Hamilton, C. D., 1965. Changes in the soil under Pinus radiata. In: Australian Forestry, Vol. 29, pp.275-289.

Hammond, A. P., Goh, K. M., Tonkin, P. J., Manning, M. R., 1991. Chemical pretreatments of peats and organic silts in a gley podzol environment: Grahams Terrace, North Westland. Soil Science Department, Lincoln College, New Zealand, DSIR Lower Hutt New Zealand. In: New Zealand Journal of Geology and Geophysics, Vol. 34: 191 - 194.

Harley, J.L., Harley, E.L. 1987. A check-list of mycorrhiza in the british flora. New Phytol. 105, 1-102.

Harris, G.P., Morrison, T.M., 1958. Fixation of nitrogen-15 by excised nodules of *Coriaria arborea* Lindsay. Nature, 182: 1812.

Harrison, A. F., Ineson, P., Heal, O.W., 1990. Nutrient cycling in terrestrial ecosystems. Field methods, application and interpretation. Elsevier applied science. pp. 454.

Harrison, S.G., Dallimore, W., Jackson, A.B., 1974. A handbook of Coniferae and Ginkgoaceae. Publ. Edward Arnold. pp.729.

Hart, P. B. S., Watts, H. M., Milne, J. D. G., 1986. Agronomic consequences of removal of topsoil from Judgeford silt loam (Typic Dystrochrept). N.Z. Soil Bureau Scientific Report No. 76, D.S.I.R. Lower Hutt.

Hatcher, P.G., Breger, I.A., Maciel, G.E. and Szeverenyi, N.M., 1985. The geochemistry of humin. in: Humic substances in soil, water and sediments, Wiley, N.Y.pp.275-302.

Hauter R., Steffens D. 1985. Einfluss einer mineralischen und symbiontischen Stickstoffernaehrung auf Protonenabgabe der Wurzeln, Phosphat-Aufnahme und Wurzelentwicklung von Rotklee. Z. Pflanzenernaehr. Bodenkd. 148: 633-646.

Haynes, R., 1982. Environmental Science Methods. Chapman and Hall, London.

Hempfling R., Schulten H. R., 1989. Selective preservation of biomolecules during humification of forest litter, studied by pyrolysis-field ionization mass spectrometry.

In: The Science of the Total Environment, 81/81: 31 - 40. Elsevier Science Publishers, Amsterdam.

Hewitt, A.E. 1992. New Zealand soil classification. DSIR Land Resources Scientific Report No. 19. Dunedin.

Hofmeister, H., 1983. Lebensraum Wald. Ein Weg zum Kennenlernen von Pflanzengesellschaften und ihrer Ökologie. Verlag Paul Parey, p. 252.

Jacks, G.V., 1934. Soil, Vegetation and Climate. Imp. Bur. Soil Sci. Techn. Comm., no.29.

Janssen, H. 1991. Shelterwood Forestry: Sustainable Land Management in Production Forestry. In: Sustainable Land Management, The Proceedings of the International Conference on Sustainable Land Management, Napier, New Zealand, Ed. International Pacific College Palmerston North. pp. 347-357.

Janssen, H. 1992. A Place for Pines. Terra Nova. The Resource Management Magazine of New Zealand. June 1992, pp.45-46.

Janssen, H. 1992. Thin end of the wedge. Shelterwood systems. Sustainable methods of developing and harvesting special purpose timber trees. Growing today, pp. 12-14.

Jenny, H. 1961. Derivation of state factor equations of soils and ecosystems. Soil Sci. Soc. Am. J. 25: 385-388.

Jenny, H. 1980. The soil resource. Origin and behaviour. Springer Verlag. pp. 377.

Johnson, P.N., 1977. Mycorrhizal endogonaceae in a New Zealand Forest. N.Z. J. of Ecol. 78: 161 - 170.

Jurgensen, M. F., Frederick, D. J., Madgwick, H.A.I., Oliver, G.R., 1985. Dry matter, energy, and nutrient contents of 8-year-old stands of Eucalyptus regnans, Acacia dealbata, and Pinus radiata in New Zealand. In: N.Z. Journal of Forestry Science, 15 (2): pp. 142-157.

Jurgensen, M. F., Frederick, D. J., Madgwick, H.A.I., Oliver, G.R., 1986. Soil development under Pinus radiata and Eucalyptus regnans plantations. In: N.Z. Journal of Forestry Science 16 (1): pp. 69-77.

Keen, F.P. 1952. Insect Enemies of Western Forests. U.S. Dep. Agric. Misc. Publ. 273: 75-126.

Keeves, A., 1966. Some evidence of loss of productivity with successive rotations of Pinus radiata in the south-east of South Australia. Australian Forestry, 30: 51-63.

Kent, M., Coker, P., 1992. <u>Vegetation Description and Analysis</u>. A Practical Approach. Belhaven Press London. pp 363.

Kim, J. I., Buckau, G., Duschner, H., Psarros, N., 1990. <u>Characterization of humic and fulvic acids from Gorleben groundwater</u>. Technical University Muenchen; University Marburg, Germany. In: Fresenius' Journal of Analytical Chemistry, Vol. 338: 245 - 252.

Kingston, J. D., 1968. <u>Some soil properties associated with good and poor regeneration growth in a radiata pine forest on Mapua hill soils, Nelson</u>. M. Ag. Sc. Lincoln College, New Zealand.

Klemmendson, J. O., 1987. <u>Influence of oak in pine forests of central Arizona on selected nutrients of the forest floor and soil</u>. Soil Sci. Soc. Am. J. 51:1623-1628.

Klemmendson, J. O., 1991. <u>Oak Influence on Nutrient Availability in Pine Forests of Central Arizona</u>. Soil Sci. Soc. Am. J. 55:248-253.

Knorr, A., 1987. <u>Ernaehrungszustand, Standortansprueche und Wuchsleistungen der Esche in Bayern</u>. Schriftenr. Forstw. Fak. Univ. Muenchen Nr. 82.

Koegel-Knabner I., Hatcher P. G., 1989. <u>Characterization of alkyl carbon in forest soils by CPMAS ^{13}C NMR spectroscopy and dipolar dephasing.</u> Institute of Soil Sciences and Soil Geography, University of Bayreuth, Germany. In: The Science of the Total Environment, 81/82: 169 -177. Elsevier Science Publishers, Amsterdam.

Koegel-Knabner I., Hatcher P. G., Tegelaar, E. W., de Leeuw, J. W., 1992. <u>Aliphatic components of forest soil organic matter as determined by solid-state ^{13}C NMR and analytical pyrolysis.</u> Institute of Soil Sciences and Soil Geography, University of Bayreuth, Germany et al. In: The Science of the Total Environment, 113: 89 - 106. Elsevier Science Publishers, Amsterdam.

Koegel-Knabner I., Zech, W., Hatcher P. G., 1988. <u>Chemical composition of the orrganic matter in forest soils: The humus layer</u>. Institute of Soil Sciences and Soil Geography, University of Bayreuth, Germany. In: Zeitschrift fuer Pflanzenernaehrung und Bodenkunde, 151: 331 - 340.

Koegel-Knabner I., Zech, W., Hatcher P. G., 1990. <u>Decomposition and humification processes in forest soils: Implications from structural characterization of forest soil organic matter.</u> Institute of Soil Sciences and Soil Geography, University of Bayreuth, Germany. In: International Congress of Soil Science (14 th. :1990: Kyoto, Japan).

Koegel-Knabner I., Zech, W., Hatcher P. G., 1991. Chemical Structual Studies of Forest Soil Humic Acids: Aromatic Carbon Fraction. Institute of Soil Sciences and Soil Geography, University of Bayreuth, Germany. In: Soil Sci. Soc. Am. J. 55: 241 - 247.

Kononova, M. M., 1966. Soil Organic Matter: Its Nature, Its Role in Soil Formation and in Soil Fertility. Pergamon Press Ltd., Oxford.

Kontchou, C. Y., Blondeau, R., 1990. Effect of heterotrophic bacteria on different humic substances in mixed batch cultures. Universite des Sciences et Techniques de Lille Flandres- Artois, France. In: Can. J. Soil Sci. 70: 51 - 59.

Koslowska, A., 1934. The influence of plants on the concentration of hydrogen ions in the medium. Journ. Ecol., Vol. 22, pp. 396-419.

Kundler, P., 1963. Einfluss verschiedenartiger Waldbestaende auf die Bodenentwicklung. Archiv fuer Forstwesen Band 12 Heft 7 pp.659-675.

Lambert, M. J., Turner, J., 1986. Nutrient Concentrations in Foliage of Species Within a New South Wales Sub-Tropical Rainforest. Annals of Botany 58, pp. 465-478.

Lampkin, N. 1992. Organic farming. pp 701. Farming Press books, UK.

Larcher, W. 1984. Oekologie der Pflanzen. Auf physiologischer Grundlage. Verlag Eugen Ulmer Stuttgart. p. 403.

Lauenroth, W. K., et al., 1993. Modelling vegetation structure-ecosystem process interactions across sites and ecosystems. Ecological Modelling, 67 49-80. Elsevier Science Publishers B. V. Amsterdam.

Ledgard, N. J., Belton, M. C., 1985. Diversification and opportunities in forestry in the South Island High Country. N.Z. Journal of Forestry, 30 (1): 133-143.

Levett, M. P., Adams, J. A., Walker, T. W., Wilson, E. R. L., 1985. Weight and nutrient content of above-ground biomass and litter of a podocarp-hardwood forest in Westland, New Zealand. N.Z. Journ. of For. Sci. 15(1):23-35.

Leyval, C., 1990. The Interactions between Micro-organisms, Minerals and Forest Tree Roots: Lysimeters in a Greenhouse. In: Nutrient Cycling in Terrestrial Ecosystems. Field Methods, Application and Interpretation. Ed. Harrison, A. F., Ineson, P., Heal, O.W. Elsevier Applied Science. Section 4; chapter 27, pp. 335 - 346.

Likens, G. E., Bormann, F.H., a.o. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook Watershed-ecosystem. Ecol. Monogr. 40: 23-47.

MacCarthy, P., Malcolm, R. L., 1989. The Nature of Commercial Humic Acids. Department of Chemistry and Geochemistry, Colorado, U.S.A. American Chemical Society 4: 55 - 63.

MacCarthy, P., Malcolm, R. L., Hayes, M.H.B., Swift, R. S., Schnitzer, M., Campbell, W.L., 1986. The establishment of a collection of standard humic substances. In: Transactions, 13th Congress International Society of Soil Science, 2, 378.

Madgwick, H. A. I., 1985. Dry matter and nutrient relationships in stands of *Pinus radiata*. In: N.Z. Journal of Forestry Science 15 (3): pp. 324-336.

Maggs, J., 1988. Organic matter and nutrients in the forest floor of a Pinus elliotii plantation and some effects of prescribed burning and superphosphate addition. In: Forest Ecology and Management, 23, pp. 105-119.

Major, J. 1951. A functional, factorial approach to plant ecology. Ecology 32: 392-412.

Malcolm, R. L., Mc Carthy P., 1991. The individuality of humic substances in diverse environments. US Geological Survey, Denver Colorado, U.S.A. In: Advances in Soil Organic Matter Research: The Impact on Agriculture and the Environment; eds. Wilson et al. University of Essex; Birmingham. pp.23 - 34.

Mark, A. F., 1979. Proceedings of the Professor G.T.S. Baylis Retirement Seminar. R.N.Z.I.H. Annual Journal No. 7. pp. 111 - 126.

Mark, A. F., 1980. Ecological Principles in Land Use Allocation. In: The Land Our Future: Essays on Land Use and Conservation in New Zealand. Longman Paul / New Zealand Geographical Society Inc., Chapter 2, pp. 17-30.

Mark, A.F., 1990. Indigenous grasslands of New Zealand. Ecosystems of the World. Vol. 8B, Natural Grasslands - Eastern Hemisphere. Edited by R.T. Coupland. Elsevier, Amsterdam. pp.361 - 410.

Mark, A. F., McSweeny, G. D., 1990. Patterns of Impoverishment in Natural Communities: Case History study in Forest Ecosystems, New Zealand. Woodwell, G. M. (Ed.) The Earth in Transition-Patterns and processes of biotic impoverishment. C.U.P., New York. pp. 151-176.

Marschner, H., Romheld, V., 1983. In vivo measurements of root-induced pH changes at the soil root interface. Effect of plant species and nitrogen source. Zeitschrift für Pflanzenphysiologie, 111, 241- 251.

Marschner, H., 1986. Mineral Nutrition of Higher Plants. Institute of Plant Nutrition; University of Hohenheim, F.R.G. Academic Press, pp. 649.

Maser, C.O. 1966. Life Histories and Ecology of Phenacomys silvicola. M.S. thesis on file, Oreg. State Univ., Corvallis.

McKellar, I.C. 1966. Sheet 25-Dunedin (1st. ed.). Geological Map of New Zealand, 1 : 250,000. DSIR Wellington.

McKenzie, D.W., Stirling, I.F. et al. 1976. New Zealand Atlas. (ed. Wards, I.) A.R. Shearer Government Printer Wellington.

Mc. Lintocks, A.H., 1949. History of Otago. Otago Centennial Historical Publication. p. 829.

McNabb, R.F.R., 1968. The Boletaceae of New Zealand. N.Z. J. Bot., 6: 137 - 176.

Meadows, D.H., D.L., Randers, J., 1992. Beyond the limits. Global collapse or a sustainable future. pp 300. Earthscan publications, London.

Metcalf, L. J., 1987. The cultivation of New Zealand Trees and Shrubs. Reed Methuen, p.346.

Mettin, C., 1986. Inwieweit ist Laubstreu eine oekologische und oekonomische Hilfe in Nadelholzbestaenden? A.F.Z. 37: 918-922.

Meurk, C. D., 1995. Evergreen broadleaved forests of New Zealand and their bioclimatic definition. Landcare Research New Zealand Ltd, Lincoln, New Zealand. in: Vegetation Science in Forestry, Kluwer Academic Publ., pp. 151-197.

Mikola, P., 1985. The effect of Tree species on the Biological Properties of Forest Soil. National Swedish Environmental Protection Board, Rapport 3017. Information Section, Box 1302, S-171 25 Solna, Sweden.

Milburn, J., 1987. Water Storage in Trees. Encyclopedia of Plantphysiology. Vol 12/3.

Miller, R.B., 1963. Plant nutrients in hard beech. N.Z. J. Sci., 6: 365 - 413.

Milligan, R.H., 1972. A review of beech forest pathology. N.Z. J. For., 17: 202 - 211.

Ministry for the Environment, 1993. Making Connections: An overview of Agenda 21. MfE, Wellington.

Ministry for the Environment, 1993. Living for the Future: A guide to Agenda 21. MfE, Wellington.

Minyard, P. L. and Driver, C.H. 1972. Initial steps in decomposition of Douglas-fir needles under forest conditions. In: Proceedings-Research on Coniferous Forest Ecosystems-A symposium.

Miodragovic, Z. M., Jokic, A., Pfendt, P.A., 1991. Fulvic acid characterization in an alluvial sediment sequence: differences between clay and sand environments. Faculty of Chemistry, University of Belgrade. In: Org. Geochem. Vol. 18, No. 4: 481 - 487.

Mollison, B., 1988. Permaculture. A Designers' Manual. Tagari publications, Australia. pp. 576.

Molloy, L. 1988. Soils in the New Zealand Landscape; the living mantle. New Zealand Society of Soil Science, New Zealand Soil Bureau; Mallinson Rendel Publ. Wellington.

Morgan, R. K., 1992. Chemical Analysis of Soil. Department of Geography, University of Otago. p.79.

Morrison, T.M., 1956. Mycorrhiza of silver beech. N.Z. J. For., 7: 47 - 60.

Muys, B., Lust, N., Granval, Ph., 1992. Effects of Grassland Afforestation with Different Tree Species on Earthworm Communities, Litter Decomposition and Nutrient Status. In: Soil Biol. Biochem. Vol. 24, No. 12, pp. 1459-1466.

Muys, B., Lust, N., 1992. Inventory of the Earthworm Communities and the State of Litter Decomposition in the Forests of Flanders, Belgium, and its Implications for Forest Management. In: Soil Biol. Biochem. Vol. 24, No. 12, pp. 1677-1681.

Nambiar, E.K.S., Squire, R.O., Sands, R., Will, G.M., 1984. Manipulations of water and nutrients in plantations of fast growing species. In: Proc. IUFRO Symp., Pretoria South Africa, Forest Research Institute, Pretoria, pp. 489-506.

New Zealand Forest Service, 1981. N.Z. Forest Service Policy on Exotic Special Purpose Species. N.Z.F.S. Wellington.

New Zealand Meteorological Service, 1963. Summaries of climatological observations at New Zealand stations to 1960. Department of Civil Aviation, Wellington.

New Zaland Native Forest Restoration Trust, 1992. The living forests of New Zealand. D. Bateman (publ.), p.224.

New Zealand Soil Bureau 1954. General survey of soils of North Island, N.Z. Soil Bureau Bull. 5 N.Z. D.S.I.R.

New Zealand Soil Bureau 1968. General Survey of Soils of South Island, New Zealand. N.Z. Soil Bureau Bulletin 27. 404p.

New Zealand Soil Bureau, 1972. Soil Bureau Laboratory Methods. Scientific Report 10.

New Zealand Soil Bureau, 1987. Methods for Chemical Analysis of Soils. Scientific Report 80.

New Zealand Soil Bureau, 1990. Soil Carbon Analysis. S 5: Organic carbon. Adaptation of the Walkley Black procedure.

Oades, J. M., 1988. Biogeochem. 5: 35-70.

O'Connell, A. M., 1987. Litter decomposition, soil respiration and soil chemical and biochemical properties at three contrasting sites in *Eucalyptus diversicolor* forests of south western Australia. In: Australian Journal of Ecology. 12, pp.31-40.

Odum, E., 1983. Fundamentals of Ecology. German transl. from the original titel. Georg Thieme Verlag, Stuttgart New York. p. 836.

Ovington, J. D., 1983. Ecosystems of the World 10. Temperate Broad-leaved Evergreen Forests. Publ. Elsevier. 241 p.

Page, A.L., Miller, R.H., Keeny, D.R., (eds.), 1987. Methods of Soil Analysis. Part 2 Chemical and Microbiological Properties. second edition.

Pardy, G., Bergin, D., 1989. Raising native hardwood trees. Preliminary research findings. Tree Grower, February 1989, pp.3-5.

Parker, R.W., Parker, A. L., 1986. Boron, lead, and zinc as contaminants in forest ecosystems: a literature review. FRI Bulletin No. 103. 75p.

Parker, S., P., ed. 1982. Synopsis and Classification of Living Organisms. Mc. Graw-Hill.

Parkinson, B., Cox, G., 1990. A field guide to New Zealand's Lakes and Rivers. Random Century. p. 176.

Parsons, J. W., 1988. Isolation of humic substances from soils and sediments. In: Humic Substances and their Role in the Environment, pp. 3 - 14. John Wiley and Sons Limited; S. Bernhard, Dahlem Konferenzen, 1988.

Poole, A. L., Adams, N. M., 1980. Trees and Shrubs of New Zealand. Hasselberg, Government Printer Wellington, New Zealand. pp 257.

Powell, A.W.B., 1987. Native animals of New Zealand. Gill (ed.) Auckland Institute and Museum. p.88.

PNAP, 1987. N.Z. Protected Natural Areas Progamme, Dunedin Ecological District. 69.02 pp. 77-8., Lands and Survey Department. Wellington.

Pryor, L. D., 1976. Biology of Eucalyptus. Studies in Biology no 61. Publ. Edward Arnold Ltd. London. 82 p.

Qualls R. G., Haines, B. L., Swank, W. T., 1991. Fluxes of dissolved organic nutrients and humic substances in a deciduous forest. In: Ecology, 72 (1), pp. 254-266.

Raeside, J.D. 1964. Loess deposits of the South Island, New Zealand, and soils formed on them. Soil bureau publication No. 310. New Zaland Soil Bureau, Dunedin.

Rafes, P.M. 1970. Estimation of the effects of phytophagous insects on forest production. In: Reichle (ed.), Analysis of temperate forest ecosystems, p.100-106.

Rasyid, U., Johnson, W. D., Wilson, M. A., Hanna, J. V., 1992. Changes in organic structural group composition of humic and fulvic acids with depth in sediments from similar geographical but different depositional environments. Org. Geochem. Vol. 18, No 4: 521 - 529.

Raunkiaer, C., 1922. Forskellige Vegetationstypers forskellige Indflydelse paa Jordbundens Surhedsgrad Brintionkoncentration, Kgl. Danske Videnskabernes Selskab, Biol. Med., p.515. (Transl. as Chap 14 of "The life Forms of Plants and Statistical Plant Geography. Oxford, 1934).

Raven, P. H., Evert R. F., Eichhorn S.,E., 1986. Biology of Plants. pp. 755. Publ. Worth Inc. N.Y.

Reichholf, J.H., 1990. Der Tropische Regenwald. Die Oekobiologie des artenreichsten Naturraums der Erde. pp 207. D.T.V. Muenchen.

Reichle, D. E., 1970. Analysis of Temperate Forest Ecosystems. Springer Verlag, 297 p.

Renbuss, M. A. , Chilvers, G. A., Pryor, L. D., 1972. Microbiology of an ashbed. Proc. Linn. Soc. N.S.W., Vol. 97, 4, 302-10.

Richter, D. D., Markewitz, D. et al., 1994. Soil chemical change during three decades in an old-field loblolly pine (Pinus taeda) ecosystem. In: Ecology, 75 (5), pp. 1463-1473.

Robb, J., 1986. New Zealand Amphibians and Reptiles. Collins, p. 128.

Roehrig, E., Ulrich B., 1991. Ecosystems of the World 7. Temperate Deciduous Forests. Publ. Elsevier. 635 p.

Rogers, H. J., Perkins, H. R., Ward, J.B., 1980. Microbial cell walls and membranes. Chapman and Hall, London.

Sarkar, A.N., Jenkins, D.A., Wyn Jones, R.G., 1979. Modification to mechanical and mineralogical composition pf soil within the rhizosphere. In "The Soil-Root

Interface" (J.L. Harley and R. Scott-Russell eds.), pp. 125 - 136. Academic Press, London and Orlando.

Scharpenseel, H. W., Krausse, R., 1961. Aminosaeureuntersuchungen an verschiedenen organischen Sedimenten, besonders Grau- und Braunhuminsaeurefraktionen verschiedener Bodentypen (einschliesslich C^{14}- markierter Huminsaeuren). Institut fuer Bodenkunde der Universitaet Bonn, Germany. Vol. 96 No.1: 11 - 34.

Schnitzer, M., 1971. Characterization of Humic Constituents by Spectroscopy. Soil Research Institute, Department of Agriculture, Ottawa, Canada. In: Soil Biochemistry Vol. 2/4.

Schnitzer, M., Skinner, S. I. M., 1967. Alkali versus Acid Extraction of Soil Organic Matter. In: Soil Science, Vol. 105 No. 6: 392 - 396.

Schroeder, D., 1984. Bodenkunde in Stichworten. Verlag Ferdinand Hirt. p.160.

Schulthess, C. P., Huang, C. P., 1991. Humic and fulvic acid adsorption by silicon and aluminium oxide surfaces on clay minerals. In: Soil Sci. Soc. Am. J. 55: 34 - 42.

Schwenk, T., 1976. Sensitive Chaos. The Creation of Flowing Forms in Water and Air. Rudolf Steiner Press, London, 1965, p.144.

Shaymukhametov, M. Sh., et al., 1984. Use of physical fractionation methods to characterize soil organic matter. Dokuchayev Soil Institute, Moscow. In: Soviet Soil Science 16; Pochvovedeniye, No. 8: 131 - 141.

Shugart, H. H., West, D. C., 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. J. Environ. Manag. 5: 161-179.

Shugart, H. H., Mortlock, A. T., Hopkins, M. S., Burgess, I. P., 1980. A computer simulation model of ecological succession in Australian sub-tropical rainforest. ORNL/TM-7029. Oak Ridge National Laboratory, Oak Ridge, Tennessee. 48 p.

Shugart, H. H., 1984. A Theory of Forest Dynamics. The Ecological Implications of Forest Succession Models. Publ. Springer Verlag. 278 p.

Simmonds, J. H., 1927. Trees from other lands for shelter and timber in New Zealand.

Smale, M.C., Oeveren, H. van, Glaeson, C.D., Kimberley, M.O., 1987. Dynamics of even-aged Nothofagus truncata and N. fusca stands in North Westland New Zealand. In: N.Z. Journal of Forestry Science 17 (1): pp. 12-28.

Smale, M. C., Bathgate, J.L., Guest, R., 1986. Current prospects for Tawa. NZFS reprint 1866.

Smith, R. T., Atkinson, K., 1975. Techniques in Pedology; A handbook for environmental and resource studies. London: Paul Elek Ltd.

Soil Survey Staff 1975. Soil Taxonomy: A basic system of soil classification for making and interpreting soil surveys. Agriculture Handbook No. 436, Soil Conservation Service, U.S. Department of Agriculture. 754 p.

Stace, C., 1991. New Flora of the British Isles. Cambridge University Press.

Stevenson, F.J., 1982. Humus Chemistry Genesis, Compositions, Reactions. University of Illinois, Dept. of Agronomy. Wiley-Interscience Publ. 437 p.

Stevenson, F.J., 1986. Cycles of Soil. Carbon, Nitrogen, Phosphorus, Sulfur, Micronutrients. University of Illinois, Dept. of Agronomy. Wiley-Interscience.

Stewart, G. H., 1986. Population dynamics of a montane conifer forest, Western Cascade Range, Oregon, USA. In: Ecology, 67 (2), pp. 534-544.

Stewart, G. H., Rose, A. B., Veblen, T.T., 1991. Forest development in canopy gaps in old-growth beech forests, New Zealand. In: ournal of Vegetation Science 2: pp. 679-690.

Stone, E. L., Will, G. M., 1965. Nitrogen deficiency of second generation radiata pine in New Zealand. In: C.T. Youngberg (Ed.) Forest-soil relationships in North America. Oregon State University Press, Corvallis.

Strand, M.A., and Nagel W.P. 1972. Preliminary considerations of the forest canopy consumer subsystem. In: Proceedings-Research on Coniferous Forest Ecosystems-a Symposium, p.71-77.

Suggate, R.P. and Stevens, G.R. Te Punga, M.t. (Eds.) 1978. The Geology of New Zealand. Government Printer, Wellington. 2 vols, 820 p.

Sweet, G.B., and Wareing, P.F. 1966. Role of plant growth in regulating photosynthesis. Nature 210: 77-79.

Swift M. J., Heal, O. W., Anderson, J. M., 1979. Decomposition in Terrestrial Ecosystems. Publ. Blackwell Scientific Publications Ltd. 372 p.; Fractionation of Soil Humic Substances. 15: 387 - 408.

Swift, R., Delisle, G., Leonard, L. R., 1987. Biodegradation of humic acids from New Zealand soils. Soil Science Department, Lincoln College, New Zealand; Dept. of Microbiology and Immunology, Queens University, Ontario, Canada. In: The Science of the Total Environment, 62: 423 - 430.

Szwagrzyk, J., Czerwczak, M., 1993. Spatial patterns of trees in natural forests of East-Central Europe. In: Journal of Vegetation Science 4: pp. 469-476.

Taylor, N.H., Pohlen, I.J. 1968. Classification of New Zealand soils. Chapter 2 in; Soils of New Zealand, Part 1, N.Z. Soil Bureau Bulletin 26.

Thomson, D., 1990. Developing Protection for Natural Areas. National Diploma in Horticulture. Subject No. 19. Dunedin Botanical Gardens.

Thomson, S.; Simpson, G., 1935. Notes on Hydrogen ion concentration of Forest Soils in the Vicinity of Dunedin, New Zealand. Transactions pp.192-200.

Thornton, R. H., Cowie, J. D., Mc Donald, D. C., 1956. Mycelial aggregation of sandy soil under Pinus radiata. Nature, London, 177: pp. 231-232.

Tomlinson ,P.R., Kennedy, N.M., Leslie, D.M., 1978. Soil Map of Dunedin city and Environs, New Zealand. Scale 1 : 31 680. N.Z. Soil Bureau Map 107 . Part of N.Z. Soil Survey Report 37.

Tomlinson, P.R., Leslie, D.M., 1977. Some environmental relationships of loessial soils in Dunedin city and environs. Soil Bureau, DSIR Wellington.

Toutain, F., 1981. Les humus forestiers, structures et modes de fonctionnement. Rev. For. Fr. (Nancy), 33(6) 446-477.

Trotter, McCulloch, 1989. Unearthing New Zealand. Published in New Zealand.

Tuckett, F. 1844. Frederick Tuckett's diary 25th to 28th of April 1844, Hocken Pamphlet 29/3, Dr T. M. Hocken's collection.

Turner J., Lambert, M. J., 1988. Soil properties as affected by Pinus radiata plantations. New Zealand Journal of Forestry Science 18 (1): 77-91.

Turner, F.J. and Verhoogen, J. 1960. Igneous and Metamorphic Petrology (2nd. ed.). McGraw-Hill, New York.

Ulrich, B. 1987. Stability, Elasticity, and Resilience of Terrestrial Ecosystems with Respect to Matter Balance. In: Potentials and Limitations of Ecosystem Analysis. Ecological Studies, Vol. 61 p.11-49.

Walter, H., Breckle S. W.,1985. Ecological Systems of the Geobiospere. Ecological Principles in Global Perspective. Publ. Springer Verlag. 244p.

Walter, H., Breckle S. W., 1987. Ecological Systems of the Geobiosphere. Temperate and Polar Zonobiomes of Northern Eurasia. Publ. Springer Verlag. 581 p.

Wardle, J., 1970. The ecology of Nothofagus solandri. N.Z. J. Bot., 8: 494 - 646.

Wardle, J., 1984. The New Zealand Beeches. Ecology, Utilization and Management. N.Z. Forest Service, F.R.I., p. 447.

Wardle, P., 1953. An ecological survey in the hill country north of Dunedin. Thesis, Otago University.

Wardle, P., 1961. Fraxinus excelsior. J. Ecol. 49: 739-751.

Wardle, P. 1972. Plant succession on greywacke gravel and scree in the subalpine belt in Canterbury, New Zealand. N.Z. J. Bot., 10: 387 - 398.

Wardle, P., 1980. Primary succession in Westland National Park and its vicinity, New Zealand. N.Z. J. Bot., 18: 221 - 232.

Wardle, P., Bulfin, M. J., Dugdale, J., 1983. Temperate broadleaved evergreen forests of New Zealand. In: Temperate Broadleaved Evergreen Forests. J.D. Ovington (Ed) Elsevier, Amsterdam, Chap.3, pp. 33-71.

Waring, R. H., Schlesinger, W. H., 1985. Forest Ecosystems. Concepts and Management. Academic Press, Inc. 340p.

Way, M. J., and Cammell M. 1970. Aggregation behaviour in relation to food utilization by aphids. In Watson A. (Ed.) Animal populations in relation to their food resources, p. 229-247.

Weber, G., Rehfuess, K. E., Kreutzer, K., 1993. Ueber den Einfluss naturnaher Waldwirtschaft auf den chemischen Bodenzustand. A.F.Z. 2 pp. 68-71.

Will, G. M., 1968. Some aspects of organic matter formation and decomposition in pumice soil growing *Pinus radiata* forest. In: 9th International Congress of Soil Science Transactions III, Paper 24, pp. 237-246.

Williams, G.R., 1973. Birds. In: G.R. Williams (ed.), The natural history of New Zealand. Reed Wellington, pp. 304 - 333.

Wilmanns, O., 1984. Oekologische Pflanzensoziologie. Quelle & Meyer Heidelberg, p. 372.

Wilson, W. S., 1991. Advances in Soil Organic Matter Research: The Impact on Agriculture & the Environment. Proceedings of conference, pp. 400.

Wittich, W., 1953. Untersuchungen ueber den Verlauf der Streuzersetzung auf einem Boden mit starker Regenwurmtaetigkeit. Schriftenr. Forstl. Fak. Univ. Goettingen u. Nieders. Forstl. Versuchsanst. Bd. 9.

Wittich, W., 1961. <u>Der Einfluss der Baumart auf den Bodenzustand.</u> Allg. Forstz. Muenchen; 16, 41-45.

Wittich, W., 1972. <u>Die Bodenpfleglichkeit der Buche.</u> Forst- u. Holzw. 27, 52-54.

Zech, W., Ziegler, F., Koegel-Knabner I., Haumaier, L., 1992. <u>Humic substances distribution and transformation in forest soils</u>. Institute of Soil Sciences and Soil Geography, University of Bayreuth, Germany. In: The Science of the Total Environment, 117/118: 155 - 174. Elsevier Science Publishers, Amsterdam.

Appendices:

Appendix: A (Text):

1   Addendum:

1.1 Geology and Geomorphology of the Dunedin Ecological District.

The Dunedin Ecological District is characterised by Pleistocene loess, covering upper Miocene to probably lower Pliocene igneous rock strata, mainly basalt and phonolite (Suggate, 1978). The oldest material in the region is a series of greywacke, thousands of metres in thickness, with basaltic tuff and pillow lava, surfacing somewhat south of the district at the Taieri Mouth. The greywacke was deposited in late Paleozoic to early Mesozoic time and was subsequently metamorphosed and deformed to produce the Otago Schists, the metamorphism being accomplished by the early Cretaceous time.

Freshwater fanglomerates, conglomerates and breccia with some plant remains, accumulated along fault scarps during the early to middle Cretaceous time. Continued erosion during the late Cretaceous resulted in the development of a peneplain (an extensive area of little relief). Swamp deposits that led to the Taratu coal formations formed on the Cretaceous erosion surface of Schists. A marine transgression submerged the Dunedin area. Near shore sediments of Glauconitic sands, pebbly limestone and fossil assemblages of plant remains, ammonites, oyster shells and belemnites were deposited in the Upper Cretaceous (Mata series) time. For most of the Tertiary the land of the Dunedin District was well submerged. Massive deposits of Mudstone (210 m thick), from the Paleocene to the lower Eocene were followed by depositions of well sorted unfossiliferous loose sand. Minerals in both the Mudstone and the sand (e.g. K-feldspar) show that its material was in part derived from a granitic terrain and probably in part from the Otago Schists (

Geology Dept. O.U. Dunedin). The deposition of further massive layers of calcareous and fossiliferous mudstone (55 m) of the Upper Eocene is followed by a paraconformity (i.e. a period of non-deposition) and subsequent deposition of fossiliferous sandstone (230 m) of the Lower Miocene. Volcanic activity commenced in the Middle Miocene times (13.1 million years; K-Ar method) when first ash showers of basaltic and trachytic tuffs interceded with sandstones and local limestone lenses of the Waipuna Bay Formation. Uplift had occurred on the west side of the Dunedin district by late Miocene. Erosion stripped much of the Cretaceous and Tertiary sediment cover from the western but not from the metropolitan area. Such erosion probably continued while sedimentation and early volcanic eruptions were proceeding in the region of the Otago Peninsula. Eruptive activity comprised four principle phases and lasted for little over 3 million years, from 13.1 to 10 million years ago (Coombs, 1987). The initial eruptive phase centred on the Port Chalmers - Portobello area and consisted of massive flows of trachyte. The middle portion of the Otago Peninsula and the lower parts of the Mihiwaka-North Head ridge derive from voluminous outpourings of basalt and some phonolite of the first main eruptive phase(Benson, 1959, 1968). Flood plain conglomerates, enclosing leaf beds separate the first from the second main eruptive phase, with flows ranging from basalt to phonolite. First phase flows are covered in the middle portions of the Flagstaff - Swampy - Cargill - Mihiwaka ridges and the upper part of the west end of the Otago Peninsula. In the youngest sub-phase two very distinctive flows, the Roslyn doleritic basalt and the Leith Valley trachyandesite are widely exposed on the west side of the complex (McKellar, 1966). Voluminous phonolite flows also form part of the second Phase, which closed with explosive eruptions and the deposition of the Younger Floodplain Conglomerate. Basalts of the third main eruptive phase cap Swampy Hill, Maori Hill and St. Clair Hill and underlie the top of Flagstaff and Mt. Cargill which are in turn capped by very voluminous phonolites also seen at Blueskin Cliffs and forming lava domes at Mt. Kettle, Mihiwaka and Wetherstone Hill. Lavas covered about 520 square kilometres in the Dunedin district and extended into surrounding areas. Erosion has since stripped the lavas from a portion of the region. The Kaikorai valley and the lower slopes of Kaikorai hill are areas within the Dunedin Ecological District where Paleocene and Eocene sedimentary rocks surface under Pleistocene aeolian deposits. In contrast to most other areas of Miocene - Pliocene volcanic rocks in New Zealand the Dunedin Volcanic Complex is distinctly alkaline in character (Coombs, 1965). Basaltic rocks include weakly alkaline types as well as basanites and varieties rich in phenocrysts of olivine, titanaugite or both. Intermediate types such as kulaite,

trachybasalt and trachyandesite are present. Phonolites, both trachytoid and nephelinitoid, are widespread and voluminous (Turner, Verhoogen, 1960); (Coombs, Wilkinson, 1969).

1.2   Flora and Fauna

The Dunedin Ecological District must have teemed with indigenous bird life prior to human settlement. This assumption is based on the diversity of habitats in the district and the high pre-European hunter-gatherer human population (see 2.5). The coastline and the topography of the district provide plenty of heterogeneous habitats. The broadleaf-podocarp forest and most of the indigenous avifauna co-evolved for millions of years and the extensive tidal areas would have provided ample sustenance for the marine fauna and the coastal, migrant and indigenous avifauna. *Petroica australis* (Robin; Toutouwai) occur in forest remnants north of Dunedin city and on Otago Peninsula. *Bowdleria punctata* (Fernbird; Matata) is present in scrub on the ranges north-west of the city. *Mohoua ochrocephala* (Yellowhead; Mohoua) have been reported from forest near Dunedin and is absent elsewhere from east of the main divide (PNAP 1987). The frugi- and herbivorous *Hemiphaga novaeseelandiae* (Native Pigeon; Kereru) finds a variety of foodsources in the indigenous and exotic vegetation and facilitates the dispersal of the few surviving specimen of the Podocarpaceae into surrounding scrub land. The insectivorous *Rhipidura fuliginosa* (Fantail; Piwakawaka) also seems to adapt to a drastically altered environment. The nectarfeeding birds *Anthoris melanura* (Bellbird; Korimako) and *Prosthemadera novaeseelandiae* (Tui) evade some of the competitive exotic pressure, by utilising a diverse range of insects and fruits as a supplementary foodsource (Falla et al. 1987). Most exotic bird species are well adapted to this new anthropoid environment, where they complete their life cycles, while *Turdus merula* (Blackbird) ventures into indigenous forest stands (Brockie 1992). The nesting site of *Diomedea epomophora* (Northern Royal Albatross; Toroa) at Tairoa Head (Otago Peninsula) is unique as the only mainland albatross colony in the world. The Otago Peninsula is also one of only two major breeding areas for *Megadyptes antipoda* (Yellow-eyed Penguin; Hoiho), as well as *Eudyptula minor* (Blue Penguin; Korora). The Tairoa heads are also important breeding grounds for *Puffinus griseus* (Sooty Shearwater; Muttonbird-Titi), *Phalacrocorax chaconotus* (Stewart Island Shag) and *Stictocarbo punctatus* (Spottet Shag). *Heteropholis gemmeus* (Jewelled Gecko) is widespread in forest remnants in the district (PNAP 1987; Robb 1986). *Galaxis*

argentus (Giant Kokopu) can be found in some streams of the area (PNAP 1987; Parkinson, Cox 1990).

1.3   Cultural contributions.

Prior to human settlement the forest around the coasts of the South Island was continuous and reached from shore to treeline. Isolated areas in the lee of the central divide were without forest cover. Natural tussock lands covered central Otago, the Mackenzie Basin and isolated areas in the Canterbury plains (Mark, 1990). Radiocarbon dating indicates that there was widespread burning of forests 500 to 800 years ago, which resulted in the loss of almost half of the original forest in a series of fires. It is acknowledged that during the first 500 years of human occupation of New Zealand, there were widespread changes to the environment that included the extinction of a number of bird species, notably all species of Moa, a giant rail, a goose, a duck and the giant eagle, and that this resulted not only from direct predation, but also as a result of habitat loss through forest fires. These environmental changes in turn necessitated major adjustments to the people's economy and accelerated alterations to their culture (Trotter, McCulloch, 1989). It is difficult to trace back the origins of the first people, who settled in the South Island due to consecutive waves of North Island Maori assimilating one way or another the culture and lore of their predecessors (McLintocks, 1949). Semi mythical traditions tell of the Kahui Tipua, fearsome supernatural beings, as the first inhabitants of the South Island. The Te Rapuwai succeeded these beings by lighting a fire at the time of the dry north-west winds, when the Kahui Tipua were asleep, and subsequently left many place names to record their presence. The Kaitangata lake district and the mouth of the Matau (Clutha) was apparently a place of settlement for these people. Little more is known about these people since no Maori claim descent from them. Almost as little is known about their immediate successors, the Waitaha. According to the lore of the North Island Maori, the Waitaha people arrived in the Takitimu canoe, one of the great fleet, 640 years ago. On the other hand certain southern genealogies of the Waitaha show them to have descended from the Uruao canoe and Rakaihaitu the great digger of the inland lakes, who came to the South Island forty-three generations, or approximately 850 years ago. It does not seem unreasonable to assume that the Waitaha of Otago were the Moa-hunters (McLintocks, 1949). The presence of obsidian in the Moa-hunters middens would indicate an early tradelink with the North Island. Around 500 years ago the Katimamoe moved south and

formed a stable southern community with the Waitaha. The move of the Ngaitahu to the South Island 300 years ago led to some confrontation with the Katimamoe, who by that time had absorbed the Waitaha. Some Katimamoe were forced to the south and west while others were eventually absorbed by the Ngaitahu (Goodall, Griffiths unpubl. report "Maori Dunedin" Hocken Library).

2 Description of Distinct Temperate Forest Ecosystems;

Natural environment, ecological distribution and characteristics of the examined tree species.

In natural conditions forests are always in a state of flux as responses are made to changing environmental factors; the static structure after which a conventional forester strives in an attempt to meet economic goals have been achieved only by a constant battle against nature. Walter, (1985).

2.1 Dynamics of New Zealand Indigenous Forest Ecosystems.

2.1.1 Classification and Distribution.

New Zealand's generally youthful landscape of high relief, diverse geology and sharp climatic gradients traditionally supports forest communities, which vary widely in composition, structure and stage of development.

P. Wardle, (1983) and J. T. Salmon, (1980) describe two main classes of native forest, broadleaf-conifer forest, representing the warm temperate element in the New Zealand flora and beech forest, representing the cool temperate element.

The broadleaf-conifer forests are subdivided into three subtypes:

a)   the broadleaf-kauri-podocarp forest, which covered much of the northern part of the North Island;

b)   the broadleaf-podocarp forest that constituted the lowland rain forests of the North Island, the central west coast, the south coast to the west of the Waiau river to lake Hakapoua and Stewart Island, as well as much of the south-east coast of the South Island;

c)   the broadleaf-beech-podocarp forest is found extensively in lowland forests along the mountain ranges, of both islands, particularly the South Island.

Pure beech forest occurs in the eastern North Island mountain ranges.

In the South Island, pure beech forest can be found along the main ranges, except for the central West Coast beech gap, usually inland from the coastal podocarp-broadleaf forest or adjacent lowland podocarp-broadleaf-beech forests, especially at mid altitudes (*N. truncata, N. fusca, N. solandri, N. menziesii*). The montane forests are dominated by *N. solandri var. cliffortioides* and *N. menziesii*. Of both species *N. menziesii* is the main representative of the beeches in the inland south eastern parts of the South Island (Wardle J.,1984).

The diverse spatial distribution patterns of forest canopy species today and in prehistoric times can be explained by the exceptional geological dynamics of both main islands during the Holocene and the steep climatic gradients due to the relief. The most recent species distribution trends are influenced mainly by biological factors, the main one being the detrimental effects of introduced mammals on the vegetation cover and species diversity.

Disturbed sites are readily occupied by exotic herbs and shrubs which, if the succession continues without interruption, will eventually be displaced by indigenous flora. Many indigenous forest plants are highly shade tolerant and enjoy an advantage over their potential foreign competitors. Exotic flora makes no headway into sound, standing native forest (Brockie, 1992).

2.1.2 Composition

The broadleaf-podocarp forest subtype, including some scattered remnants of *N. menziesii* covered most of the Dunedin Ecological District, up until about one hundred and fifty years ago (Wardle,1953).

The lowland forest structure is quite diverse.

On local alluvial fans *Dacrycarpus dacrydioides, Plagianthus regius* and *Prumnopitys taxifolia* often formed the canopy, towards the coast *Metrosideros* species joined in and generally *Weinmannia racemosa* could be found with *Podocarpus hallii* as a canopy or subcanopy species. Frequent emergent species were *Prumnopitys ferruginea* and *Dacrydium cupressinum* and, further north, *Podocarpus totara*.

The broadleaf-conifer forest class includes the *Phyllocladus* species, which joins the emergent storey from the north of the South Island, as do two species of *Libocedrus*, which can also be found growing tall in Westland and Southland (Salmon, 1980). *Agathis australis* becomes a locally dominant tree north of 38° S.

The next storey at 15 to 25 m usually composes the main canopy with mostly broadleaf genera such as *Weinmannia, Elaeocarpus, Metrosideros* and in northern

districts *Beilschmiedia, Knightia, Laurelia, Litsea* and *Nestegis* each contributing one or two species.

The subcanopy (5 to 15 m) is formed by species belonging to the genera *Griselinia, Melicytus, Myrsine, Pittosporum, Pseudopanax, Pseudowintera, Schefflera* and, in the north, *Dysoxylum.*

Very common are species of the treeferns *Cyathea* and *Dicksonia* and in mild districts the palm *Rhopalostylis sapida.*

The genus *Coprosma* is most abundant in the shrub layer (1 to 5 m).

Coprosma species are joined in the south by species of *Melicope, Myrsine, Neomyrtus, Pseudopanax*, from Westland north by *Alseuosmia* and *Geniostoma*, amongst others.

Others include initially slow growing, opportunistic and shade tolerant species of the above mentioned canopy - and emergent trees.

The ground layer (less than 1 m) is usually well covered with large ferns such as *Asplenium, Blechnum, Hypolepis, Lastreopsis, Polystichum, Pneumatopteris* and *Todea.*

Herbaceous vascular plants include species of *Dianella, Libertia, Microlaena, Parietaria, Uncinia* and north of 41° S, *Elatostema* and *Australina.*

Nertera is a genus of coprosma and shares the lowest stratum with *Hymenophyllaceae* and bryophytes.

Synusia can be exceptionally well developed. Epiphytes include bryophytes, filmy ferns as well as larger ferns (*Asplenium, Pyrrosia*), vascular plants such as the lilies *Astelia* and *Collospermum*, several orchids and shrubs such as *Griselinia lucida, Senecio kirkii* and *Pittosporum cornifolium.*

Weinmannia racemosa and *Metrosideros robusta* frequently begin life as an epiphytic shrub on treeferns or other suitable hosts.

Lianes are abundant and form the much of the canopy in some forests.

They belong to the genera *Clematis, Freycinetia, Metrosideros, Muehlenbeckia, Parsonsia, Ripogonum, Rubus* and *Tetrapathaea*, and also include the ferns *Lygodium* and root-climbing species of *Blechnum, Phymatosorus* and *Rumohra.*

Despite the luxuriance of lowland conifer-broadleaf forest, most genera contain only one to two species; only *Blechnum, Coprosma, Hymenophyllum, Pseudopanax* and *Uncinia* have more than ten forest species (Wardle, P., 1983).

The structure and composition of the Beech forests becomes simpler the higher the latitude and altitude and the poorer the soil conditions.

Montane, subalpine stands of *Nothofagus solandri var. cliffortioides* or

N. menziesii form a dense canopy at 10 to 15 m and provide an extreme contrast to the lowland forests described above. Only scattered *Coprosma* shrubs, *Dracophyllum* species, lichens, bryophytes, two species of parasitic plants (*Alepis flavida* and *Peraxilla tetrapetala*) and two ferns (*Hypolepis millefolium* and *Polystichum vestitum*) cohabit the harsh environmental conditions of the montane beech forests.

However the number of accompanying species increases along gradients towards moister or warmer climates.

A forest of *Nothofagus fusca*, 30 m tall, can have *Dacrydium cupressinum* as a scattered overstorey, *Podocarpus ferrugineus* in the main canopy, a sparse subcanopy with *Weinmannia racemosa*, and a ground fern layer of *Blechnum discolor*, with other small trees and shrubs well represented, including *Carpodetus serratus*, *Coprosma spp.*, *Pseudopanax spp.*, *Pseudowintera colorata*, *Myrsine divaricata* and *Rubus cissoides* (Wardle, et al., 1983).

2.1.3 Dioeciousness and Monoeciousness.

A remarkable phenomenon of the broadleaf-conifer forest is the large number of dioecious plants. About half the trees in our native forests are dioecious, which prevents the risk of inbreeding during their long lives, and ensures that every seed produced is genetically unique, and that a plant's progeny contains a wide range of variants (Brockie, 1992). Among the wind-pollinated trees the *Podocarpaceae* are mainly dioecious, while *Agathis australis* and *Nothofagus* are monoecious. Other dioecious plants include the *Coprosma* species, the climber *Clematis paniculata* a. o.(Wardle P., et al., 1983)

2.1.4 Phenology and Nutrient Cycling.

The Orongorongo research project (from 1966 to 1990) provides important information on the dynamics of a local broadleaf-podocarp-beech forest community, which is fairly representative to the types of forest that covered most of New Zealand. Some of the findings allow interesting comparisons with data collected overseas.

The primary productivity was measured by the litterfall for the broadleaf-podocarp forest (Daniel, 1975; Cowan, et al. 1985); and independent from this project for

Nothofagus forest by (Bagnall, 1972; Wardle, J., 1970). In lowland stands of *Nothofagus solandri* and *N. truncata* litter fall amounted to between 4.9 and 6 t/ha/year, with peak falls in winter or spring. In subalpine *N.solandri* stands it ranged from 3.7 t at 1050 m to 3 t/ha/year at timberline, with leaf fall mainly during summer and autumn. In 1971 and 1972, the annual litter fall was 5.9 and 7.8 tonnes respectively, on each hectare of a mature *Metrosideros-Dacrydium* forest.

Substantial quantities of leaves fell in every month with rises in spring and summer (200 to 500 kg/ha/month) and less leaves falling in winter (about 50 to 120 kg/ha/month). An average leaf fall of 3,2 tonnes,o.d./ha/year was likely to be fuelled by a living leaf biomass of at least 6.6 tonnes/ha.

The annual leaf litterfall of this mature *Metrosideros- Dacrydium* forest compares favourably with European *Quercus; Quercus - Carpinus* (3.2 t/ha/yr.) and *Fagus* forests (2.7t/ha/yr.), but falls short of the 4.7 tonnes of leaf litter produced annually by an American *Castanea- Quercus* forest.

Seral communities of *Coriaria* and *Aristotelia* have been shown to produce 10.1 t/ha/yr. of oven dried leaf litter, which is suggestive of the importance of these pioneer species in the rapid creation of an organic soil layer.

Flowers contributed a large proportion (about 4 %) of the year's litterfall, rising to 12 % of the November sample.

Fruit and seed fall was measured contributing from 3 kg/ha in August rising to 80 kg/ha in June.

The difference of 1.9 tonnes of litter fall from 1971 to 1972, hints at the importance of periodic and irregular flowering and fruiting events, even though much of this difference might have been caused by fallen logs or branches.

The best known periodic flowerers are the four beech species and *Phormium tenax* as well as nine species of alpine tussock, which usually flower synchronously. The amounts of beech seed may fluctuate 3000-fold between poor and mast years at two to four year intervals. Weaker and less regular periodicity affects seed fall in *Dacrydium cupressinum* (Franklin, 1968 and other podocarps (Beveridge, 1964; 1973), while the flowering display of *Metrosideros* varies markedly from year to year.

The native faunal populations are closely connected to fluctuations of the native plant phenology.

About 7 tonnes of fresh litter are added annually to an estimated 143 tonnes of litter per hectare under the *Metrosideros - Dacrydium* forest (Daniel, 1975).

It is further estimated that half of the annually added leaf litter decomposes within 15 months and half the woody litter in 23 years.

The chemical nutrients contained in the litter were analysed by Daniel and Adams, (1984).

Carbon compounds, Cn ; Hn ; On , contributed presumably about 97 % of the litter weight. The macro- and micro- nutrients were analysed as contributing 135 kg/ha/year or about 3 %. Of this amount the major nutrients - calcium, nitrogen, potassium and magnesium - account for 94 %.

The trace elements - manganese, iron, zinc and copper add 1.5 % to this total. Calcium was the most abundant macro- nutrient in the litter with 51 kg/ha/year. Most of the nitrogen fell as leaf litter and was measured as contributing 44 kg/ha/year. The top 11 cm of soil contains 0.49 % of nitrogen by weight, with less at greater depths. These amounts contrast with large quantities of nitrogen shed by some shrub or immature plant communities. Tree-top lichens are probably responsible for boosting the nitrogen in New Zealand forest soils. Foliose and crustose lichens contain nitrogen fixing blue-green algae and these grow profusely as epiphytes in most mature native forests. In beech forest of the Ureweras these lichens contribute 10 kg nitrogen/ha/year (Brockie, 1992). The cycling of phosphorus in most forests is tight.

In an undamaged forest a very large percentage of the phosphorus is tied up in the vegetation and very little washes away in soil leachate.

2.1.5 Symbioses and Mycorrhizae.

Most native trees, shrubs, ferns and liverworts harbour mycorrhizae, which help in the uptake of phosphorus (Johnson, 1977), and other nutrients in exchange for carbohydrates from the plants. *Nothofagus*, like *Fagus*, has ectomycorrhizas (Morrison, 1956). The rest of the vascular flora, except the sedges and rushes, is normally in symbioses with vesicular-arbuscular endomycorrhizal fungi. In *Leptospermum* ectomycorrhizal symbionts are common alternatives (McNabb, 1968) and they have even been recorded on ferns in special circumstances (Cooper, 1976).

Root morphology and growth rate mainly determine the degree of this dependence. It is complete in the podocarps and *Agathis* in which the ultimate rootlets are concentrated into nodules that accommodate the symbionts, and also in species like *Coprosma robusta*, *Griselinia littoralis* and *Weinmannia racemosa*, in which root hairs are lacking or poorly developed. This dependence is less complete in species with hairy roots, especially if their growth is slow. Examples are *Metrosideros umbellata* and the

ferns (Baylis, 1975). *Sophora* is the only legume in New Zealand forests and is confined to lake shores, river banks, dry open forest and forest margins. *Coriaria arborea*, which often has a place in successions leading to forest, has efficient nitrogen fixing nodules (Harris, and Morrison, 1958).

2.1.6 Allelopathy.

Allelopathy of native vegetation was examined by Froude, (1980). Generally ferns and native conifers evinced stronger allelopathic effects than flowering plants, and dicotyledonous plants were more effective than monocotyledons.

2.1.7 Fauna.

The native faunal composition has been subjected to extensive changes, with the rate of extinctions and replacement by introduced mammals, birds, and insects peaking in recent history. The land birds are relatively few in species, but high in endemicity. According to Williams (1973), 36 species are primarily associated with forest. Though few of these have become extinct, several are highly endangered and fewer than a dozen can be found in fair abundance through most of the remaining forests. Besides competition for food, the main dangers ensue from predation by introduced stoats, cats and dogs.

Of 10 introduced bird species, only the blackbird (*Turdus merula*) is well established in virgin forest, the others frequenting margins and disturbed areas.

Most forest birds are insectivorous and frugivorous and as such face competition with a large number of introduced rodents.

From the native birds of prey only the morepork will hunt rodents, besides its usual diet of wetas and other insects and spiders. The bush falcon probably hunt mostly endemic forest birds.

Seed-eaters include parakeets, kaka and introduced finches (Beveridge, 1964), as well as rodents.

Nectar is an important food for several native birds for example the stitchbird, bellbird and tui. Competition for this food comes mainly from introduced insects like wasps and bees.

The New Zealand pigeon, kokako, kakapo and takahe eat foliage and so, apparently, did moas. The role of the latter in forest ecology would be interesting to know, particularly in view of the currently massive changes wrought by recently introduced mammals; possum, red deer, wapiti, sika deer, white tailed deer, fallow deer, sambar, moose, chamois, cattle, horse, goat, sheep, rabbit, hare, rodents.

The only native mammals are two species of forest inhabiting, omnivorous bats, which both are now scarce (Powell, 1987).

Reptiles are represented by some 40 species of small lizards (*Gekkonidae* and *Scincidae*) and the remarkable *Tuatara* from the group *Rhynchocephalia*, surviving on some off-shore islands. The only amphibians native to New Zealand are three species of frogs (Robb,1980), which inhabitat forest covered streams and damp forest sites. Most native fresh water fish of the species *anguilla*, *galaxias* and *gobiomorphus* have their natural habitat in streams, lakes and swamps that are surrounded by forests (Parkinson, 1990).

The most striking feature of the invertebrate fauna (Dugdale, 1977) of the New Zealand temperate forest are:

a) the immense complexity of the fauna associated with fallen plant material, fungi and bryophyte flora;

and b) the fact that less than 10 % of this endemic, diverse, irreplaceable fauna survives replacement of the indigenous plant cover by the common exotic grass or pine monoculture.

The complexity suggests that the fauna has co-evolved over an extremely long time with the forest. New Zealand forest insects can be conveniently divided into phytophages and saprophages. The arboreal phytophage insect fauna in New Zealand forests is impoverished. Wetas have largely been exterminated by introduced rodents. Only the tree wetas, *Hemideina* spp., have withstood predation and still feed together with rodents on large proportions of fallen tree seeds (Bieleski, 1959; Beveridge, 1964).

All *Nothofagus* species are subject to invasion by three Platypus species (Coleoptera: *Scolyctidae*), which introduce pathogenic fungi to stressed trees (Milligan, 1972). There is also a regular cycle of epidemics of an *oecophorid* moth, *Proteodes carnifex* on *Nothofagus solandri var. cliffortioides*, possibly leading to the local replacement of Mountain beech by the *Proteodes* immune *Nothofagus menziesii*. The only other regular defoliator epidemics known are those of *Epiphryne undosata* on the subalpine tree *Hoheria glabrata*. The impoverished phytophage fauna may be a reflection of Pleistocene events.

The saprophages however may be regarded as essentially a Tertiary fauna (Wardle P., et al., 1983). There are sixteen orders of terrestrial insects, with some 3000 species in Coleoptera alone, as well as abundant molluscs, several crustacean *orders* (*Cladocera*, *Ostracoda*, *Isopoda* and *Amphipoda* amongst others), primitive spiders and

harvestmen (*Cyphophthalmi*). The forest floor also supports such relicts as *Peripatus*, the huge ear-wig-like dipluran *Heterojapyx* and earthworms that can attain 140 cm in length. A feature shared with Australia is the presence of a sizeable element of litter-inhabiting *Lepidoptera*; over 150 species, or about 11% of the total indigenous *Lepidoptera*, have litter-feeding larvae. Peculiar to New Zealand is a smaller percentage of moths with larvae that feed in dead wood. The dominant litter-feeding family, here and in Australia, is *Oecophoridae*, with *Cremnogenes* (77 spp.) dominating in New Zealand (Wardle P. at al.,1983).

2.1.8 Soils.

The soils that supported most of the original forest cover of the North Island and the eastern part of the South Island were yellow - brown earths of moderately low fertility (Wardle, P. et al. 1983).

There were also forested yellow - brown loams, of moderate to high fertility and red granular loams and clays, as well as yellow brown pumice soils on the central plateau in the North Island. Today nearly all of these have been cleared to pasture.

Fertile forest soils occurred locally and included recent alluviums and colluviums, and soils derived from basalt and limestone.

No forests of viable size have survived the clearance on these soil types in recent history.

The remaining native forest is pedogenically marginalized and usually covers sites with a low to very low soil fertility or unevolved mountain soils, the latter usually under *N. menziesii* or N. *solandri var. cliffortioides*, except in the beech gap on the Westcoast, where *Metrosideros, Libocedrus* and *Weinmannia* cover mountainous soils.

The poorest soils are old podzolized yellow - brown earths, podsols and gley podzols. The latter have developed at the Westcoast of the South Island in areas of high rainfall on late Pleistocene moraine hills and gravel outwash terraces. In Northland, most of these soil types have been cleared despite their infertility, because of the relentless extraction of *Agathis australis*.

Some species show a broad amplitude of tolerance to soil conditions, *Dacrydium cupressinum, Nothofagus spp.* and many shrubby pioneer species.

The whole forest composition gives however an indication of the limited range of variability in the fertility of the remaining forest soils. Among lowland conifers *Dacrycarpus dacryoides, Prumnopitys taxifolia* and *Podocarpus totara* indicate recent and therefore usually fertile soils, whereas *Agathis australis, Phyllocladus spp.* and

Podocarpus hallii are most abundant on poor soils. Where *Beilschmiedia tawa* and *Weinmannia racemosa* overlap in distribution, the former grows on and possibly maintains more fertile sites than the latter. Adams (1976) demonstrated that the distribution pattern of *Nothofagus* species is correlated with decreasing soil fertility in the following order: N. fusca > N. menziesii > N. truncata > N. solandri var. cliffortioides. This relationship is broadly reflected in foliar nutrient concentrations, especially of nitrogen and phosphorus.

2.1.9 Successions.

Sites for plant succession are constantly provided, since New Zealand is a tectonically active region with high relief, notwithstanding the potential opportunities provided by past human clearances. One of the best dated primary succession is on moraine and gravel outwash, deposited during the fluctuating retreat of the Franz Josef Glacier (Wardle, P., 1980). Shrub seedlings become established among pioneer herbs and mosses, leading to dominance, first of *Carmichaelia grandifolia*, and by 30 to 40 years, of *Olearia avicenniaefolia*. By this time, there are many hardwood seedlings and forest ferns in the undergrowth, and by 100 years or so *Metrosideros umbellata* and *Weinmannia racemosa* can form forest, which in turn harbours seedlings of podocarps.

At 1000 years, these podocarps can become an overstorey of massive trees. In this area the youngest surfaces supporting "climax" broadleaf-conifer forest, characterized by maximum complexity and an understorey of *Blechnum discolor*, are dated at 5000 years, and their soils are mapped as yellow-brown earths.

The chronosequence of vegetation and soil development as examined by Stevens and Walker, 1970 at Franz Josef Glacier found that nitrogen, organic carbon and organic phosphorus was increasing to a steady state for 12 000 years. The extreme climatic conditions of very high precipitation at this part of the Westcoast soon leads to the formation of gleys and podzols and the net loss of nutrients from the ecosystem after more than 12 000 years. *Dacrydium cupressinum* is adapted to these worsening soil conditions and forms dense stands. Ultimately further deterioration would lead to heath and bog vegetation after 22 000 years.

The succession to beech forest can be much simpler. In a subalpine situation, for example, seedlings of *Nothofagus solandri* became successfully established on river gravel, deposited four years earlier and could be expected to lead to a mature stand within 200 years (Wardle, P., 1972).

These chronosequences are specific to these sites.

Less extreme humid or cold temperate climates would allow a diverse climax forest association to store nutrients more efficiently in the soil and hence remain at a productive, quasi steady state for much longer periods of time (Walter, 1985).

A comparison with tropical forest ecosystems on nutrient poor base material shows a different strategy. Most nutrients are stored in plants and cycled between plants with mycorrhizal fungi. Limited amounts of atmospheric and pedogenic nutrient inputs never permitted any surplus production and hence explain the poor soil development, as well as the scarcity of herbivores and carnivores (Reichholf, 1990).

2.2 Dynamics of the Temperate Deciduous Forest Biomes.

Due to a self imposed completion deadline for this thesis the section on the deciduous forests will not be discussed in as much detail as the section on the indigenous and coniferous forests. However there is abundant published research material, which allows for an indepth comparison between the typical features of the deciduous forests and those of the indigenous forests, the temperate and boreal coniferous forests and the "fringe forest systems", containing predominantly species that are best adapted to marginal sites.

Detailed relevant information on the temperate deciduous forests has been discussed and referenced in chapter 8 and general information was published by (Hofmeister, 1983; Odum, 1983; Waring, Schlesinger, 1985; Delcourt, 1987; Walter, 1985, 87; Roehrig, Ulrich, 1991; Dengler, 1992).

The temperate deciduous forest biome of the Northern Hemisphere occupies the northeastern parts of North America and sweeps across Europe as a broad band from the Atlantic in the west to the Ural mountains in the east. Then it disappears into the steppes and deserts of central Asia, to reappear again around the Yellow Sea and in northeastern China. Southward into central China it used to merge with a broadleaf evergreen forest complex, as it did in America and Europe, prior to human induced deforestation. Some species maintain the deciduous habit in the temperate broadleaved evergreen forest ecosystems of the Southern Hemisphere (South America, New Zealand, Tasmania) and in the temperate coniferous forest ecosystem of the North American West Coast.

The exotic deciduous trees of this study originate from the European and North American temperate forest biome.

2.2.1 *Acer pseudoplatanus*

Acer pseudoplatanus reaches 15-30 m height and naturally occurs, as a typical member of mixed forest, in the east-, central and south European mountainous regions. In the Harz moutains it grows to heights of 800 m, reaching 1600 m in the Alps. Species that typically associate with *Acer pseudoplatanus* include *Acer platanoides*, *Fraxinus excelsior*, *Ulmus spp.*, *Prunus avium*, *Tilia cordata*, *T. platyphyllos*, *Sorbus torminalis*.

Acer pseudoplatanus withstands long periods of time in the shade as a sapling, and is capable of withstanding periods of drought, but requires plenty of light and average soil nutrient contents for rapid growth. The root system has a heart shaped form. The initial growth of *A. pseudoplatanus* is faster than that of *Fagus sylvatica*, but with age, the size difference diminishes.

There is a high demand for *Acer pseudoplatanus* timber in all sizes. It machines well and has a wide variety of uses. Acer-Fraxinus associations may be found on steep rocky surfaces and in moist gullies, where *Fagus sylvatica* can not outcompete either species. (Dengler, 1992).

2.2.2 *Aesculus hippocastanum*

Aesculus hippocastanum has a rather restricted natural distribution, which would have been persistent since the Pleistocene. It originates from the mountainous regions of the south-western Balkan (Albania, northern Greece), and has been introduced widely to the gardens and parks of Europe. There is no available literature on the disposition of *Aesculus hippocastanum* in its natural habitat. It reaches a height of 30 m and has a broadly columnar shape. (Dengler, 1992; Coombes, 1992).

2.2.3 *Fagus sylvatica*

Fagus sylvatica reaches a height of 15 - 40 m and has a natural distribution, covering West- and Central Europe and the mountainous regions of South- and south-eastern Europe, from where *Fagus orientalis* takes its place of distribution further east to Anatolia and the Caucasus mountains. Since the cooling of the Subatlanticum (from 4500 years B.P.) *Fagus sylvatica* has become the dominant tree in this region, where it frequently forms pure stands, on acidic and alcaline substrate.

It typically develops a heartshaped root system. Compared to other broadleafed trees, the litter of *F. sylvatica* decomposes with some resistence. The percentage of litter decomposition per annum is dependent on the mineral availability of the substrate and may vary from 7 - 10 % to over 50 - 65 % per year. Despite the inclusion of large amounts of Ca in the litter, (Wittich, 1953, 1972) *Fagus sylvatica* can not generally be regarded as a species that improves soil quality, due to the nature of the organic compounds in the litter.

The dominance of *Fagus sylvatica* in Central Europe's forests is based on its shade tolerance and shading ability. Saplings are able to grow at 20 % of full light and are well adapted to the limited light conditions within a *F. sylvatica* dominated forest. Its American relative *Fagus grandifolia*, associates freely with other species in mixed mesophytic forests. (Dengler, 1992).

2.2.4 *Fraxinus excelsior*

Fraxinus excelsior may reach heights of up to 40 m, within 100 years and volumes of 700 Vfm/ha (Knorr, 1987). Its distribution covers central Europe from southern Scandinavia to Sicily and extends from Ireland and northern Portugal to the Wolga river and the Caucasus mountains in Russia. In central Europe it reaches altitudes of 700 m in the Harz mountains and 1600 m in the Alps.

Fraxinus excelsior is a typical tree of mixed forests and frequently grows in association with *Tilia*, *Ulmus*, *Acer* and *Quercus*. Such associations were widespread throughout Central Europe during the warmer and moist Atlantic period (7500 - 5000 years B.P). Today, *Fraxinus excelsior* grows well in association with *Acer* in the moist submontane regions, with *Alnus*, *Populus*, *Acer* and *Salix* on river alluvium and with *Acer*, *Tilia*, *Ulmus* on alcaline rocky substrate in steep river valleys.

Fraxinus excelsior is a light demanding tree. As a sapling it may however survive periods in shady conditions (at up to 7-9% of full light).

The root system covers a wide area and penetrates the soil to a medium depth. An early and well developed rootsystem ensures resistance against desiccation, during periods of drought or on limestone substrate. However, *Fraxinus excelsior* requires sufficient water during the growth period (at > 100 days per year) for rapid increases in volume. The elemental concentrations of P, Ca, N and Mg in leaf litter are higher in the ash when compared to *Fagus sylvatica*. *Fraxinus excelsior* may produce 10 kg of seed every second year, which may disperse to around 125 m (Wardle, 1961).

According to the Central European mythology, the ash tree is the ancestor of the human male gender and was regarded as the tree that symbolizes the earth axis by forming a heavenly connection to the Polar star.

Timber of *Fraxinus excelsior* is in high demand at all size classes, due to its exceptional elastic qualities and its uniform colour. Historically, its elastic qualities made it the ideal timber for cart wheel spokes. Today it is sought after in the automobile industry and for the manufacture of furniture, tool handles and sport goods. (Hofmeister, 1983; Dengler, 1992).

2.2.5 Quercus canariensis

Quercus canariensis originates from the Atlas mountains in northern Africa and also occurs in southern and north eastern areas of the Iberian peninsula. It reaches a height of 25 m and has a broadly columnar shape. (Coombes, 1992; Flora Britannica).

2.2.6 Quercus robur

The distribution of *Quercus robur* is rather similar to that of *Fraxinus excelsior*. Its southern limits are the Italian peninsula and the Balkan, except Greece and Anatolia. Its optimal site conditions are situated in the river lowlands of Central Europe. In the Harz mountains it reaches 600 m altitude, in the Alps it grows up to 1200 m.

Quercus robur reaches heights of up to 40 m and naturally requires plenty of light throughout its life. *Quercus robur* is undemanding with regard to the nutrient condition of the substrate and achieves good root penetration even in dense and compacted soil types with its pole shaped root system.

Oak used to have a prominent position in European mythology in connection with the forces of lightning. Its acorns used to provide food for wild pigs and domesticated stock. Its timber was used for cart wheel rims, house building and for boat building. Entire oak forest regions were destroyed, in the historical quest for imperial dominance.

Today, oak timber is in high demand from medium to high quality and size. Oaks have been grown both as a "Niederald" with a short rotation and production of 10 Vfm/ha/yr and as "Hochwald" for the production of strong timber (at 5-7 Vfm/ha/yr) and acorns. If grown as a "Hochwald" oaks need a dominant position (light requirements) in a mixed forest with species like *Tilia cordata* and *Carpinus betulinus*. (Hofmeister, 1983; Dengler, 1992).

2.2.7 Quercus rubra

Quercus rubra is one of the fastest growing oaks and reaches heights of 30 m. It has a wide natural distribution, covering the central eastern parts of North America, including the catchments of the upper Mississipi, the lower Missouri, the great Lakes (except the northern shore of Lake Superior), the Ohio and the Appalachian mountains. *Quercus rubra* is a very adaptable and versatile tree, but grows best in the climate and soil-nutritional conditions of the Ohio valley and the western slopes of the Alleghenies, where it naturally grows in mixed mesophytic forests.

As a juvenile, *Quercus rubra* survives under limited light conditions of 15-30%, but requires plenty of light for optimal growth, like other oaks. The timber quality is

comparable to that of the european oaks. *Quercus rubra* may be established at lower densities and requires less care than the european oak, due to its rapid growth rate. (Brockman, 1979; Hofmeister, 1983; Dengler, 1992).

2.2.8 *Tilia europaea*

Tilia europaea is an artificial hybrid of *Tilia cordata* and *Tilia platyphyllos*, and has been planted widely in parks. It may reach a height of 25 - 30 m. The natural distribution of *Tilia cordata* is very similar to that of *Quercus robur*. The centres of distribution are in the Balticum, eastern Prussia, parts of the north-west German lowlands, the Lower Rhine area, the Pfaelzer Wald and the Vogelsberg in Hessen. These areas are characterized by a reduced competition from *Fagus sylvatica*, due to cold winters, limited summer moisture, or high ground water tables. *Tilia platyphyllos* naturally grows in drier conditions, compared to *Tilia cordata*.

Tilia cordata initially grows slower, compared to *Fraxinus excelsior* and *Acer pseudoplatanus*, but regains lost height with age. It is shade tolerant, regenerates well, and typically grows in mixed associations with *Quercus robur*, *Q. petraea*, *Fraxinus* and *Acer*.

The age of Linden trees can be considerable (up to 1000 years).

Flowering Linden trees attract human lovers. The flowers are also well known for their medicinal qualities and as a source of honey. The leaf litter decomposes very well. The timber is light, good to work with and has a wide variety of uses as a special purpose timber. (Hofmeister, 1983; Dengler, 1992).

2.2.9 *Ulmus x hollandica & Ulmus procera*

Ulmus procera or *Ulmus minor var. vulgaris* is the English elm.

Ulmus x hollandica is a hybrid between *Ulmus glabra* and *Ulmus minor*. Hybridizations between species are very frequent for the genus *Ulmus*, and have caused some difficulties with regard to the classification of species. *Ulmus glabra* has a similar east-west distribution, but grows somewhat further north (Scandinavia, Russia) and south (Greece) compared to *Quercus robur*. In the Harz mountains it reaches an altitude of 700 m, in the Alps it grows up to 1400 m. It reaches a height of 30 m and grows initially faster than *Fraxinus* and *Acer*. As a sapling it can survive the shady conditions of a mixed species forests.

The rootsystem reaches deep in the form of a heart shaped pole root. The litter readily decomposes, due to high contents of cations and a beneficial C/N ratio.

In Central European mythology, women were thought to have descended from the elm tree. Elm woods were indicators of fertile sites that could support agriculture. The elm leaves used to be a major food source for wild and early domesticated cattle.

The timber of elms is very sought after. It is as strong as that of oak and very resistant to splitting. It has been used for the manufacture of wheel hubs. Today, elm timber is used for boat building, the manufacture of furniture and sports goods. (Coombes, 1992; Dengler, 1992).

2.3 Dynamics of Coniferous Forest Ecosystems

2.3.1 Classification, Distribution and Composition.

The major primary producers of the global coniferous ecosystems belong to the class of the *Pinatae* or Conifers. *Pinatae* belong to the division of *Pinophyta* or gymnosperms, which are the first seed bearing plants and comprise three subdivisions.

The living fossils of the *Cycadicae* comprise only one class, the *Cycadatae* and one family, the *Cycadaceae*. *Cycadicae* were first recorded in Permean sediments and formed a major part of Triassic ecosystems. The subdivision of the *Gneticae* consists of three widely divergent sub-classes, each with a single family whose relationship to other gymnosperms is not clear. The subdivision of the *Pinicae* contains two classes.

The *Ginkgoatae* is a class with a single species, which can be traced back in fossil records to the Permian epoch. It was widely distributed in the Jura epoch.

The second class comprises the *Pinatae* or conifers. Conifers first evolved about 300 million years ago in the late Carbon epoch.

Seven surviving families of the class of the *Pinatae* constitute the coniferous ecosystems of the Earth. The largest class of extant gymnosperms includes only one extant subclass, the *Pinidae* (fossil and extant species). The extant *Pinidae* are usually divided into at least two orders, the *Pinales* and the *Taxales*. A third order, the *Cupressales*, is sometimes recognized for the *Cupressaceae* and the *Taxodiaceae*.

The *Pinales* include seven families: The *Araucariaceae* contain 30-40 species combined in two genera, *Araucaria* being dioecious and *Agathis* being monoecious.

The *Podocarpaceae* combine eleven genera and about 130 species, most of which are dioecious and predominantly native to the southern hemisphere.

The *Taxodiaceae* comprise about 17 species, derived from ten monoecious genera, three of them native to North America and seven genera are native to Asia and \ or Tasmania.

The other four families are native to the northern hemisphere and include:

The *Cephalotaxaceae* (7-8 species, mostly dioecious) and native to temperate eastern Asia;

the *Cupressaceae* (eighteen genera and about 140 species, monoecious to dioecious);

the *Taxaceae* (five genera and about 19 to 22 species, mostly dioecious) and

the *Pinaceae* with ten genera and about 215 to 250 monoecious or dioecious species (Parker, et al., 1982).

Generally the climate-ecological amplitude of the southern hemisphere conifers is much narrower, when compared to the northern hemisphere conifers. The former is characterized by an even, moist climate and a relatively low yearly amplitude of temperature, while most genera of the latter are characterized by an adaption to a high annual amplitude of temperature and precipitation. This trend is reflected in substantial differences in habitat size and climates in both hemispheres, due to the distribution of continents and oceans. An independant evolution of both, northern - and southern hemisphere conifers has been in existence since the Jura, possibly even the Permean age (Floges, 1980; Florin, 1940).

2.3.2 Southern Hemisphere conifers.

The distribution of conifers in the subtropical and temperate southern hemisphere, was far more extensive in the Mesozoic and Tertiary eras compared to the Quarternary era. The main genetic pool of the southern conifers at the beginning of the Cenozoic seemed to have been centred on the landmass of New Zealand, from where three temporally and spatially different migrations of species occurred (Floges, 1980; Dawson, 1958).

The Antarctic provided a landbridge to South America at the beginning of the Cenozoic (Floges, 1980; Schmithuesen, 1960, 66).

Southern conifers migrated to the forming Indonesian archipelago, via Australia and the islands of Micronesia in the mid - and late Tertiary era (upper Miocene, early Pliocene). They established a new genetic centre within the angiosperm dominated tropical and subtropical mountain forests, at a time when sclerophyllous *Eucalyptus* and *Acacia* forests replaced much of their old habitats in Australia. Concurrently the northern conifers that had migrated from Asia, possibly via mountain ranges in the

Phillipines, became extinct in Borneo, as the high moutain ranges that provided climatic refugia eroded away and submerged into the tropical forest zone (Floges, 1980; Müller, 1965 - 75).

The recent range of distribution of southern hemisphere genera covers parts of South America, subtropical parts of south east Asia, as well as the entire Indonesian archipelago and Oceania, where gymnosperms reach their greatest diversity of species and genera (Groombridge, 1992).

2.3.3 Northern Hemisphere conifers.

The highest genetic diversity in the temperate zone is found in Asia, followed by North America and Europe. This is true for gymnosperms as well as angiosperms.

Many genera of gymnosperms that found refuge in south east Asia during the Pleistocene were distributed throughout the northern hemisphere in the Tertiary era. In North America a number of genera that are adapted to warm and moist temperate climate, survived the climatic adversities of the Pleistocene along the wide, north - south oriented valleys of the coastal western mountain ranges, including the Cascades and the Sierra Nevada. The orogenesis took place in the late Tertiary era and definetely led to an independant evolution of the eastern and western flora by blocking oceanic influences, that previously reached to the Rocky Mountains, which initially divided a rather homogenous angiosperm, gymnosperm flora from the mid-Tertiary era (Daubenmire, 1978).

The entire area of the north west conifer biome is climatically characterized by a dry period during summer (one to five months) and a wet winter period.

Sequoia sempervirens, Picea sitchensis, Abies grandis, Thuja plicata and *Tsuga heterophylla* form temperate rain and fog forests north of 37o latitude along the Pacific coast.

2.3.4 *Pseudotsuga menziesii* and associated flora.

Just to the east, the forests are formed by *Tsuga heterophylla, Thuja plicata* on moister sites and *Pseudotsuga menziesii* on drier sites. This area extends to the western slopes of the inland Cascade range and the Sierra Nevada south to 36o latitude. The montane forests in this region are covered by *Abies amabilis, A. procera, A. grandis, Pinus monticola* and *Pseudotsuga menziesii. Pseudotsuga* has the widest range of habitat. It is common to differentiate the *coastal P. menziesii var. menziesii,* from the inland variety *P. menziesii var. glauca* (Dengler, 1992). The former variety is found west of the Cascades and the Sierra Nevada and is part of a mixed forest, including

coniferous *Abies*, *Thuja* and *Tsuga* species and the western angiosperms, *Quercus garryana*, *Fraxinus oregona*, *Alnus rubra*, *Acer macrophyllum*, *Populus trichocarpa* and circumboreal *P. tremuloides*. The latter variety, *Pseudotsuga menziesii var. glauca*, grows in higher altitudes in the Rocky Mountains from Idaho to northern Mexico, mixed with *Picea engelmannii*, *Abies concolor*, *Abies magnifica* and *Pinus ponderosa*, *P. contorta* and *P. lambertiana*. *Pseudotsuga menziesii var. menziesii* grows together with *Sequoiadendron giganteum*, *Abies* and *Pinus* species in the western uplands of the Sierra Nevada, altitudinally just above a region of Californian Oaks. The great ecological variance within the area of distribution explains the existence of numerous morphological and ecological types of *Pseudotsuga menziesii*. Even on a small scale differences of relief and aspect cause clear genetic variability in phenological features (Campbell, Franklin 1981). Saplings of *P. menziesii* grow well in light shade and are usually the first to establish on disturbed areas. The nutrient requirements are not high, as long as there is sufficient warmth and water. The oceanic conifers reach their most complex form of evolution in the Puget Sound, Mount Olympus area, 48o N ; 123o W, +/ - 1o. *Tsuga heterophylla*, *Thuja plicata* and *Abies grandis* are the dominant forest trees here, with *Pseudotsuga menziesii* occurring on drier sites. (Odum, E., 1983). There is an abundance of sub-canopy vegetation and epiphytic bryophytes.

2.3.5 Nutrient Cycling.

The consumer system of a temperate coniferous biome in Oregon, is composed of a series of grazing and detritus food chains.

In the forest canopy most consumers are insect grazers, which feed mainly on new tissue from expanding needles or leaves (Keen 1952).

A second group of primary consumers includes insects with sucking mouth parts. They act as physiological sinks and remove dissolved nutrients from the xylem sap (Way, Cammell 1970).

Only one vertebrate foliage feeder has been reported in the forest canopy, the red tree mouse (*Phenacomys longicaudus*)(Maser 1966).

Plant reproductive tissue are also consumed, mainly by cone and seed feeding insects. Mature seeds may be consumed prior to dissemination by certain bird species and squirrels.

Omnivorous birds use seeds as a primary food source during the winter.

Predators and parasites constitute the next link in the food chain. Small invertebrates are consumed generally by other invertebrates, such as spiders and insects. Parasitic forms may feed on larvae, pupae, or eggs of the host. During the mating and nesting season, omnivorous birds feed on insects, with egg hatch being correlated with peak insect abundance. Predation of adult birds is rare, but nest predators may be found consuming both eggs and young nestlings. Other predatory birds are also rare components of the forest canopy; however the spotted owl (*Strix occidentalis*) is an important predator of vertebrate foliage feeders.

Although the consumption of foliage or cones is not considered at a rate to affect production in the old growth canopy, the preferential consumption of new needles and expanding cones may affect the nutrient capital of the trees. These consumption sites are physiological sinks, and mobile nutrients are actively moved to them from senescent foliage and storage sites within the trees (Sweet, Wareing 1966).

The loss of these sinks may mean the return of certain nutrients to the soil solution rather than their retention by the trees (Rafes 1970).

The canopy foodchain may influence the energy flow rates within the detritus food chain by the quality of its detrital outputs (Strand 1972).

The detrital food chain outputs, as well as the throughfall and the quality of the litterfall (Abee, Lavender 1972) determine the composition of the soil fauna and the formation of humic exchange sites for nutrient uptake by fungal hyphae or roots. More amounts of of N, P, and Ca were transferred to the soil through litterfall than through throughfall, while more K ad Mg were added to the soil through throughfall (Abee, Lavender 1972).

Studies on the nutrient budget of a wet *Pseudotsuga menziesii* forest, west of the Cascade mountain range showed that this forest system retains nitrogen quite effectively.

An annual nitrogen gain of 0.5 kg/ha was measured.

Phosphorus outflow from the forest was similar to that of nitrogen and amounted to an annual net loss of 0.25 kg/ha.

Cation input in precipitation was less than 10 percent of sources from mineral weathering-indicating that mineral weathering was the principle source of cations to the system.

Minimum estimates of annual net losses of calcium, sodium, magnesium and potassium were: 47, 28, 11 and 1.5 kg/ha, respectively. Silica loss of 99 kg/ha was the largest of all constituents.

The losses of the cations are approximately four times those reported for the Hubbard Brook, broadleaf deciduous forest ecosystem in New Hampshire (Likens et al. 1970), except for the potassium values, which were nearly equal to those reported in the *Pseudotsuga menziesii* forest (Fredriksen, 1972).

Other studies were aimed at decomposition processes in wet *Pseudotsuga menziesii* forests and showed a 60% mass reduction of annual organic matter production over one year. Several genera of fungi are capable of decomposing waxes on the surface of needles during the first 6 months following litterfall. The process of increasing solubility of cellulose and saccarides follows in the second 6-month period (Minyard, Driver, 1972).

A large percentage of nutrients is tied up in the enormous biomass of the producers, as is the case with tropical rainforests (Reichholf, 1990).

This, tragically has led to the illusion of exploitable abundance in both biomes in the past.

Today it has become clear that conventional timber extraction methods, such as clearfelling, are not ecologically sustainable in the oceanic conifer biome (Odum, E., 1983).

2.3.6 *Cryptomeria japonica.*

Cryptomeria japonica belongs to the *Taxodiaceae.*

The *Taxodiaceae* are an old and once widespread family of gymnosperms. The family appeared in the fossil record about 150 million years ago and is represented today by widely scattered species that are the remnants of populations which were much more widespread during the Tertiary period.

A feature shared with the *Podocarpaceae* is the restricted distribution around the oceanically influenced warm-temperate and humid parts of the continents. The family comprises ten genera and about 17 species, mostly distributed around the Pacifc region of the northern hemisphere, with the one exception of two species of *Athrotaxis*, which grow in Tasmania. The genera *Sequoia, Sequoiadendron* and *Taxodium* are native to North America. The genera *Cryptomeria, Cunninghamia, Metasequoia glyptostroboides, Sciadopitys* and *Taiwania* are native to Asia.

Cryptomeria japonica grows to a tall forest tree in Japan, attaining heights of 30 m.(Baumeister, 1975; Brockman, 1979; Parker, 1984.)

The oceanic coniferous forests of North-west America and eastern Asia, differ floristically and ecologically from the widespread continental conifer forests of the boreal biomes of the northern hemisphere.

There is no equivalent of a boreal biome in the southern hemisphere.

While the *Taxodiaceae* cover 10 genera including *Sequoia*, and the *Cupressaceae* contain 18 genera including *Thuja*, all other coniferous genera of the temperate rain - and fog forests of the American north west belong to the *Pinaceae*, as do all of the coniferous trees of the boreal biome in Eurasia and America.

2.3.7 The Pinaceae and the Eurasian boreal biome.

Only four genera of the *Pinaceae* cover the vast areas within the circum-polar belt of the boreal zone, which extends south of the Arctic forest boundary in continental northern Asia and America. In lower latitudes, *Pinaceae* also occur widely in high altitude orobiomes. The corresponding climate is humid, with temperature means above 10 celsius ranging from 120 days, the minimum requirement for many hardwood deciduous trees, to 30 days, the approximate minimum for *Picea spp.*, *Larix* and boreal *Pinus* and *Abies spp.* (Walter et al. 1985). Within the boreal zone these species can cover vast areas as single species forests, commonly on podzol soils. However the angiosperm genera *Betula*, *Populus*, *Salix* and *Alnus* are important throughout the boreal biome by forming riparian vegetation and initial successional stages that definitely improve the generally poor soil quality (Mikola, 1985).

The transitional zone to the deciduous temperate forests is rather broad in Europe, America and eastern Asia. Certain species of *Quercus, Tilia, Acer, Ulmus* and *Corylus* are cold hardiest and appear furthest to the north. The pattern of species distribution depends largely on differences in the degree of continentality and cold resistance.

Oceanic influences with heavy snow falls in winter allow *Pinus* and *Betula spp.* to form forests in coastal Scandinavia and the Kamchatka peninsula.

Larix dahurica forms pure larch forests in the extreme continental climate of mountainous eastern Siberia, where it forms a zonal vegetation type, the "light taiga".

West of the Jenisej, quasi pure stands of *Abies sibirica* and *Picea obovata* form the "dark taiga" of the Ob lowlands, which extends west of the Ural mountains into the extreme north east of Europe.

Picea, *Abies* and *Larix* species form distinct areas of zonal vegetation throughout the northern taiga zone.

2.3.7.1 The Pinaceae and the North American boreal forests.

The boreal forests in North America and Eurasia are very similar in the low number of species and genera, with the latter being the same in the boreal forests of both continents.

However the zonal vegetation types are not as marked in North America, because of a lower climatic variance. *Picea glauca* dominates the boreal zone of North America, with *Picea mariana* occupying wetter sites. The mountainous north west is covered mainly by *Picea engelmannii*. Hybrids with *Picea glauca* are common within the western boreal zone.

2.3.8 Phenlogy .

The frequency of fruiting in the boreal forests depends on annual climatic variations that can alter the period of vegetative growth quite significantly. This in turn has a major effect on the faunal food chain, with the seed eating avifauna and the rodents, *Sciurus* (squirrels) and *Clethrionymus* (voles) multiplying rapidly after years of good seed harvest, which in turn benefits the carnivorous fauna.

2.3.9 Symbioses and Mycorrhizae.

The *gymnospermae* are usually mycorrhizal.

The *Cupressaceae* and *Taxaceae* possess vesicular-arbuscular mycorrhiza,(Harley, 1987) as do species of the southern Hemisphere *gymnospermae* (Mark-Baylis, 1979 Department of Botany; University of Dunedin).

The *Pinaceae* are ectomycorrhizal, although there are some recent records of the occurrence of vesicular-arbuscular mycorrhiza.

Some may have ectendomycorrhiza in the seedling state in nurseries, but develop ectomycorrhiza later (Harley, 1987).

2.4 Coniferous pyrophytes.

2.4.1 The genus Pinus in the boreal forest biome.

Pinus banksiana is common in the transition zone between mixed deciduous - coniferous forests and the boreal zone in North America (Eyre 1980).

Pinus species are generally far less common in the boreal forests of America, when compared to Eurasia.

The most widespread conifer in Eurasia is *Pinus silvestris*. This tree does not form part of a zonal vegetation type, but merely fills gaps and forms an ecocline series (Walter, 1985).

Pinus silvestris and other species of the genus *Pinus* are pyrophytes. They cohabit niches in fire induced successional sub-climax associations, as well as beside the association of *Picea sphagnosa* on oligotrophic raised bogs, as *Pineta sphagnosa*, within the boreal zone (Walter, 1985).

Pinus species maintain their presence in almost pure stands in areas that are subjected to frequent litter fires, which tend to destroy saplings of *Picea* and *Abies*, the climax zonal vegetation, as well as co-pioneering *Betula* and *Populus* species.

Alcaline ash residues are washed out immediately by rain on lightly sandy soils, thus deteriorating the quality of the substrate (Walter, 1985).

The less frequent crown fires may initiate even aged stands of pines, which maintain a sub-climax between 100 to 150 years, after the suppression of angiosperm co-pioneer species of *Betula*, *Populus*, *Salix* and *Alnus*, which quickly establish in disturbed areas, due to their efficient adaption of seed distribution by wind and water.

A striking feature of *Pinus* species in Eurasia and America is their extensive tolerance level to environmental variables, such as to limitations of soil nutrients and moisture.

Natural disasters like biomass mineralization through fire (and economic wood extraction activities) encourage the opportunistic capability of *Pinus* species and their wider distribution.

2.4.2 The genus Pinus in the Temperate Forest Biome.

Pinus species fringe the temperate forest zone by sharing the climatic ecocline between temperate forests and steppes or boreal forests.

Within the temperate forest zone they occupy edaphic extremes.

In lower latitudes and altitudes, where climatic factors are of less relevance, *Pinus spp.* form part of sandy or rocky pedobiomes, wherever the physiological advantages of angiosperms can be balanced by a higher level of tolerance to edaphic extremes.

These can be areas of sandy podzols derived from pleistocene glacial outwash terraces, or from holocene aeolic depositions that form dunes (Walter, 1985). On other nutrient poor soils that may be ancient and leached and derived from granit or sandstone or on raw, dry substrates, derived from limestone, *Pinus* species often maintain a presence, interspersed with deciduous angiosperms.

Periodically recurring forest fires, fuelled by *Pinus* litter, may also support the temporal occupation of habitats.

The undergrowth beneath *Pinus* species is generally sparse and may consist of a herbaceous layer that is adapted to soil moisture deficits, low pH and low nutrient availability (*Pineta vaccinosa*). Especially in *Pinus* pedobiomes on poor sands or shallow granite soils, the undergrowth often consists only of lichens (*Pinetum cladinosum*), because the pines utilize all available soil water, thus preventing the growth of herbaceous species (Walter, 1985).

Pinus radiata's distribution coincides with edaphically marginal sites at the coast of the oceanic conifer biome. The limited range of *P. radiata* is possibly due to sufficient precipitation, which disabled the pyrophytic strategy of *Pinus radiata* and favoured the dominance of other conifers and angiosperms.

2.4.3 Temporal and spatial succession of the genus Pinus in eastern North America.

Research into the temporal succession of tree genera, including *Pinus*, during the late Pleistocene and the Holocene, revealed an interesting fourth dimension in species dynamics and strategies in eastern North America (Delcourt, 1987).

During the full glacial interval, pine populations reached the highest mean values of the late Quaternary (46% to 52%). Maximum reconstructed values for paleo-dominance of Pinus genera at 20,000 years before present were 81% to 88%.

Between 12,000 yr B.P. and 9,000 yr B.P., mean and maximum values for pine reached their lowest values in the late Quarternary, coinciding with major climatic changes and a floral shift in which the pine population was divided by deciduous forest into a northern and a southern group.

During the last 8,000 years the southern pines increased the total area of habitat by 14%, yet there has been an increase of 679% in the area dominated by 20% or more southern pines.

The northern pines both expanded in the total distributional area and increased in the area occupied by the intermediate dominance classes in the mid-Holocene

interval. By 500 years B.P., however northern pines decreased in total distributional area, at which time their lowest dominance class (0-20%), represented 59% of their dominance structure.

The decrease of the northern pines during the late Holocene thus contrasts with the late-Holocene expansion in southern pines (Delcourt, 1987).

2.5 Natural ecological distribution and characteristics of the sampled australian tree species.

2.5.1 The genus Eucalyptus and the species *Eucalyptus regnans*.

Eucalyptus regnans is confined to the cool temperate regions of Victoria, east of Melbourne and Gippsland and to Tasmanias north eastern and south eastern regions. It reaches heights of over 100 m in sheltered deep mountain valleys, which makes it the tallest angiosperm on earth. *Eucalyptus regnans* typically grows in somewhat open pure stands and prefers deep loams (Boland, 1985).

The genus *Eucalyptus* is native to the Australian continent, New Guinea the Bismarck Archipelago and the southern and eastern Sunda Islands from Flores and Timor to Celebes and Mindanao.

Fossil records of the genus are almost all of late Tertiary or recent age.

About 600 species dominate 95 % of Australias forest area and spread out over much of the remainder of the country.

Eucalypts have been able to adapt to a wide range of conditions in both tropical summer-rainfall and cool temperate winter-rainfall areas. Many species exist on less than 4 cm of rain a year. Eucalypts belong physiologically to the group of plants adapted to withstand drought stress, like the *Cactaceae* in America and the *Euphorbiaceae* or *Liliaceae* in Africa and Asia.

While those are generally stem or leaf succulents the *Eucalyptus* strategy differs in that the plants develop much hard tissue, -sclerenchyma- which confers to them the ability to endure, without lasting damage, severe and permanent wilting.

In a paradoxical way eucalypts do not economize in the use of water but have wide-ranging root systems and an ability to extract water from the soil even though soil moisture tension is higher than that at which more mesophytic plants can extract water.

Transpiration rates remain high even though water supply from the soil is dwindling and it is only when severe permanent wilting occurs that there is stomatal closure with some species, which inhibits further water loss (and prevents gas exchange and photosynthesis) and enables the plant to survive a critical water balance situation for some time.

Soil water extraction pressures of up to 50 bars have been recorded for eucalypts (Milburn, 1987).

At the time of human arrival in Australia the Eucalyptus vegetation was already certainly a fire adapted type.

Features had evolved, such as lignotubers, concealed buds, effectively protected cambium, heavy seed rain after hot fire, which made them well suited to an environment in which fire (dependent on lightning) was a regular characteristic.

While most *Eucalyptus* species are such well equipped, *Eucalyptus regnans* and six other eucalypt species possess an alternative strategy. These species form the wet sclerophyll forests and are generally less resistant to fire in the adult stage than the great majority of eucalypts.

They have no lignotubers so that young seedlings or treelings sustain lethal damage even from light fires and adult *Eucalyptus regnans* are often killed by an intense fire.

As a compensating condition, these species carry heavy crops of fruit in most years, from which the seed rain is very intense after a fierce fire. The conditions in wet sclerophyll forest lead to large accumulations of burnable material, which eventually lead to an intense fire, which in turn produces very favourable conditions for dense seedling regeneration.

This typically leads to even aged stands and of a different age from adjoining stands by rather large time intervals.

The microbiological recolonization of a soil following a fire induced heat sterilization follows a distinct pattern, with bacteria being at first almost exclusively present to which actinomycetes are added after a few weeks, while some seven or eight months after the fire fungi become a most prominent component of the soil microflora (Renbuss, Chilvers, 72).

This has implications for the availability of the generally limiting nutrients of nitrogen and phosphorus. The greatest contrast in growth response following a fire is seen on the sites of lowest phosphorus content. Eucalypts are very sensitive to the soil nutrient status, especially when young.

Generally however eucalypts are able to endure very low levels of many of the minor elements, which would lead to nutrient deficiencies in other plants, like clovers and even pines.

This potential is a reflected in the low natural nutrient levels of the Australian continent. Only a very limited number of *Eucalyptus* species is capable of surviving highly calcerous soil conditions or heavy textured soils with high pH values.

Ectotrophic mycorrhizae have been found in all eucalypts examined.

Eucalyptus regnans and other species of the sub-genus monocalyptus seem to be very dependent on certain endemic mycorrhizal symbioses, which seems to be the cause of failed overseas plantings and rather restricts their distribution to few other places than their natural habitat in Victoria and Tasmania, Australia. (Baumeister, 75; Brockman, 79; Forests Commission Victoria, 84; Parker, 84; Pryor, 76).

2.5.2 *Acacia melanoxylon.*

Acacia melanoxylon has a wide natural distribution, covering the cool, wet to warm, semi-humid coastal areas of Tasmania. Victoria and New South Wales.

Its form varies from a small mountain shrub to one of the largest Acacias in Australia (Boland, 1985).

Acacia melanoxylon attains its optimal growth form in the wetter, low-lying parts of north-west Tasmania, where it attains heights of 35 m and diameters of 1 - 1.5 m (Clifton, 1990). Here it grows in association with *Nothofagus cunninghamii, Dacrydium franklinii,* the southern Taxodiaceae *Atherotaxis selaginoides, Atherosperma moschatum, Eucryphia lucida* and *Phyllocladus aspleniifolius.*

This forest association has never evolved under the influence of fire.

In Gippsland, south Victoria *Acacia melanoxylon* grows in association with *Acacia dealbata, Nothofagus cunninghamii* and *Acmea smithii,* but adjacent to a forest association of *Eucalyptus regnans , Eucalyptus obliqua* and *Eucalyptus viminalis.*

In other areas *Acacia melanoxylon* grows in association with *Eucalyptus. Acacia melanoxylon* is undoubtably able to regenerate in the dappled shade of Eucalyptus from suckers and its shed seed after fires.

The adult leaf structure is sclerophyllus, rather like that of the eucalypts. Many *Acacia* species are undoubtedly pyrophytic by necessity.

If the ontogeny is a reflection of the phylogeny, then *Acacia melanoxylon's* co-evoluton with the mainly pyrophytic *Eucalyptus* genus is a phylogenetically recent event.

In this sense *Acacia melanoxylon* has a unique ecological distribution, by covering two distinct forest ecosystems, which generally are mutually exclusive in regards to canpoy species composition. (Forests Commission Victoria, 84.)

Because *Acacia melanoxylon* attains its optimal growth form in association with pyrophobic vegetation, the tree may not primarily be associated with the pyrophanerophytes.